THE UNIVERSITY *of* EDINBURGH

Kinematics of Cricket Phonotaxis

Georgios Petrou

Doctor of Philosophy

Institute of Perception, Action and Behaviour

School of Informatics

University of Edinburgh

2012

Abstract

Male crickets produce a species specific song to attract females which in response move towards the sound source. This behaviour, termed phonotaxis, has been the subject of many morphological, neurophysiological and behavioural studies making it one of the most well studied examples of acoustic communication in the animal kingdom. Despite this fact, the precise leg movements during this behaviour is unknown. This is of specific interest as the cricket's ears are located on their front legs, meaning that the perception of the sound input might change as the insect moves. This dissertation describes a methodology and an analysis that fills this knowledge gap.

I developed a semi-automated tracking system for insect motion based on commercially available high-speed video cameras and freely available software. I used it to collect detailed three dimensional kinematic information from female crickets performing free walking phonotaxis towards a calling song stimulus. I marked the insect's joints with small dots of paint and recorded the movements from underneath with a pair of cameras following the insect as it walks on the transparent floor of an arena. Tracking is done offline, utilizing a kinematic model to constrain the processing. I obtained, for the first time, the positions and angles of all joints of all legs and six additional body joints, synchronised with stance-swing transitions and the sound pattern, at a 300 Hz frame rate.

I then analysed this data based on four categories: The single leg motion analysis revealed the importance of the thoraco-coxal (ThC) and body joints in the movement of the insect. Furthermore the inside middle leg's tibio-tarsal (TiTa) joint was the centre of the rotation during turning. Certain joints appear to be the most crucial ones for the transition from straight walking to turning. The leg coordination analysis revealed the patterns followed during straight walking and turning. Furthermore, some leg combinations cannot be explained by current coordination rules. The angles relative to the active speaker revealed the deviation of the crickets as they followed a meandering course towards it. The estimation of ears' input revealed the differences between the two sides as the insect performed phonotaxis by using a simple algorithm. In general, the results reveal both similarities and differences with other cricket studies and other insects such as cockroaches and stick insects.

The work presented herein advances the current knowledge on cricket phonotactic behaviour and will be used in the further development of models of neural control of phonotaxis.

Acknowledgements

First and foremost, I would like to thank my supervisor Barbara Webb for her guidance, support and encouragement throughout this project. I would like to thank her especially for her patience and understanding during the last months of my studies and for letting me work on the stick insect robot. I would also like to thank my second supervisor Berthold Hedwig for valuable comments and helpful suggestions. My visit to his lab during my first year has inspired many of the ideas presented herein. I would like to thank the third member of my committee Subramanian Ramamoorthy for always asking the right questions.

I would like to thank my examiners Jeremy Niven and Taku Komura for their suggestions and comments to improve this thesis.

I would like to thank the Informatics technicians Hugh Cameron, Douglas Howie, Gilbert Inkster and Robert MacGregor for constructing most parts of the experimental setup and for all their help to make the rest of my crazy ideas come true. Additionally, I would like to thank Robert for our collaboration on the Intelligent Autonomous Robotics course and the stick insect project.

I would like to thank John Bender and Ty Hedrick for sharing their tracking software. Even though I ended up using neither of them they helped me improve my own approach. I would like to thank OpenCV developers and community for such a great library. I would like to thank Sergey Bochkanov the main developer of ALGLIB for his help and for sharing his library.

I would like to thank Stefan Schöneich and Mark Payne for showing me how to prepare the crickets for experiments.

I would like to thank Michael Mangan for proofreading this document.

I would like to thank my office mates, fellow PhD students, IPAB members for our everyday interactions and especially iPub members for our Friday evening pub meetings.

On a more personal note, I would like to thank my friends in Edinburgh and back home for making these years a pleasant experience.

Finally, I would like to thank my sister Julie for taking care of our home while I was away and my parents Ioannis and Foteini for their unconditional love and support throughout these years.

My research was funded by the University of Edinburgh, EPSRC, the University of Edinburgh Development Trust and was supported by the free coffee machines in the Informatics Forum.

P.S. I feel that I should apologize for all the horrible things I did to the crickets. Nevertheless, it was all in the name of science.

To my family

“We hope that, when the insects take over the world, they will remember with gratitude how we took them along on all our picnics.”
–Bill Vaughan

And forget about the experiments we did to them, I would add.

Declaration

I declare that this thesis was composed by myself, that the work contained herein is my own except where explicitly stated otherwise in the text, and that this work has not been submitted for any other degree or professional qualification except as specified.

I confirm that the work submitted is my own, except where work which has formed part of jointly-authored publications has been included. My contribution and the other authors to this work has been explicitly indicated below. I confirm that appropriate credit has been given within the thesis where reference has been made to the work of others.

(*Georgios Petrou*)

Chapter 3 is based on work from the following jointly-authored publication:

Petrou, G., Webb, B., Detailed tracking of body and leg movements of a freely walking female cricket during phonotaxis. Journal of Neuroscience Methods, 203(1):56-68.

I conceived, designed and performed the experiments, wrote the software and analysed the data. Most of the technical work was done by Hugh Cameron, Douglas Howie, Gilbert Inkster and Robert MacGregor and the rest by me. I wrote the paper with Barbara Webb and we corrected it based on recommendations from two anonymous reviewers.

Table of Contents

List of Figures

List of Tables

List of Abbreviations

AEP	Anterior Extreme Position
AN1	Ascending Neuron 1 of the cricket auditory system
AN2	Ascending Neuron 2 of the cricket auditory system
ASA	Active Set Algorithm
CNS	Central Nervous System
CoM	Centre of Mass
CPG	Central Pattern Generator
CS	Contralateral spiracle
CSV	Comma Separated Values
CT	Contralateral tympanum
CTr	Coxo-Trochanteral joint
DoF	Degrees of Freedom
FL	Front left leg
fps	frames per second
FR	Front right leg
FTi	Femoro-Tibial joint
GA	Genetic Algorithm
HL	Hind left leg

HR	Hind right leg
IS	Ipsilateral spiracle
IT	Ipsilateral tympanum
LED	Light Emitting Diode
MDF	Medium density fibreboard
ML	Middle left leg
MR	Middle right leg
ON1	Omega Neuron 1 of the cricket auditory system
ON2	Omega Neuron 2 of the cricket auditory system
PEP	Posterior Extreme Position
RMS	Root mean square
SD	Standard Deviation
SRI	Syllable Repetition Interval
ThC	Thoraco-Coxal joint
TiTa	Tibio-Tarsal joint
TrF	Trochanteral-Femoro joint
XML	Extensible Markup Language

Chapter 1

Introduction

Insects combine remarkable locomotion abilities with a variety of exceptional sensing capabilities. Think for example of the speed of a running cockroach (Delcomyn, 1971), the height and distance a locust jumps (Bennet-Clark, 1975), the moth's sense of smell (Kennedy and Marsh, 1974) and the visual response of flies (Autrum, 1958). With less than one million neurons (compared to billions of neurons in mammals) insects exhibit a wide variety of behaviours such as communication (Von Frisch, 1967), nest building (Franks et al., 1992) and prey pursuit (Olberg et al., 2000). Their comparatively small nervous system allows the identification of specific neurons related to a behaviour and model entire circuits. Additionally, they have more stereotyped behaviours than vertebrates, making experiments easier to reproduce (Maye et al., 2007). Finally, techniques such as amputations can be employed, which are considered unethical on other animals.

All these features have attracted the attention of scientists from different fields such as biologists and engineers. Some insects are more specialised in particular behaviours and therefore are preferred for the relevant studies. For instance, ants and bees in navigation (Wehner, 2003; Srinivasan et al., 2000), crickets for sound communication (Huber and Thorson, 1985), cockroaches and stick insects for walking (Mu and Ritzmann, 2005; Cruse and Bartling, 1995) and locusts for jumping (Heitler and Burrows, 1977).

Studies usually focus either on the sensor processing or the motor output. But how does an insect convert a sensory input to motor output in order to produce a specific behaviour? And how does the motor output affect the sensor input in return? These two fundamental questions are the main motivation behind this study. To address these questions I conducted a behavioural investigation on the acoustic communication of crickets (figure 1.1), in which the precise details of leg and body motion in response to

sound were tracked.

It has been almost a century since Regen (1913) by using a telephone, proved that the auditory communication between a male and a female cricket is independent of visual, olfactory and tactile stimulus. Female crickets are able to recognise the singing patterns of conspecific males and move towards them. This behaviour is one of the most well studied processes of auditory communication in the animal kingdom, including behavioural experiments *e.g.* Bailey and Thomson (1977), neuron recordings *e.g.* Boyan (1980) or both *e.g.* Staudacher and Schildberger (1998). Most research has focused on the sound processing and the walking direction but not the movements of the legs. Yet leg movement is doubly interesting in this behaviour, not only as the mechanism by which directional changes are actuated, but also as the location of the cricket's auditory organs on their forelegs, the perception of sound is directly influenced by walking. Current information available about the leg movements during phonotaxis is limited to the description of the walking patterns (Murphey and Zaretsky, 1972), limited joint movement information (Baden and Hedwig, 2008) and tarsi positions (Witney and Hedwig, 2011).

Figure 1.1: Female (left) and male (right) cricket. Photo taken by Hugh Pastoll.

1.1 Research Aims

Current information on cricket's leg movements during phonotaxis is far from complete. The purpose of this work is to contribute towards the understanding of the interaction between auditory perception and motor action in crickets and the phonotactic

behaviour in general. More specifically the goals of this dissertation are:

- To conduct behavioural experiments on female crickets while they perform free walking phonotaxis and obtain more detailed kinematic information. For this purpose a new tracking methodology is devised, implemented and assessed.
- Analyse the data obtained for the individual joint, leg and body movements of the insect. Compare the results with previous studies and other insects.
- Estimate the auditory input that the insect receives during phonotaxis.

1.2 Thesis Outline

The rest of this dissertation is divided into four chapters:

Chapter 2 surveys the current literature by incorporating the current knowledge on the morphology, methodology, neurophysiology and modelling aspects of phonotactic and walking behaviour, mainly for the crickets but also other insects.

Chapter 3 describes the methodology followed to investigate the auditory-motor interaction. A new type of arena was created along with custom made circuitry augmenting commercially available high speed cameras.

Chapter 4 presents an analysis based on collected data following the proposed methodology. The analysis covers joint, leg and body movements, leg coordination, angles relative to the sound source and an estimation of the ears input and the effect on the movements of the insects.

Chapter 5 concludes the thesis by summarizing the results and presenting future work aspects regarding improvements on the methodology, further experimentation and modelling of the behaviour in simulations and robotic platforms.

Chapter 2

Background

2.1 Introduction

In the previous chapter, I briefly introduced the subject and the goals of this dissertation. In this chapter, I review the relevant background information to this study, with a particular focus on the cricket literature. When necessary, I will incorporate knowledge from other insects, especially regarding walking. I begin by introducing the cricket species I will concentrate on, its key features and explain basic concepts of phonotactic behaviour including information about the song used for communication (section 2.2). Then, I describe the basic morphology of the insect incorporating its motor system and various sensors, including its auditory system (section 2.3). Next, I present the different experimental strategies used to study walking and phonotaxis (section 2.4) and I include the current knowledge of the aforementioned behaviours (section 2.5). Then, I summarize the basic neurophysiology information with respect to the location and function of the neurons (section 2.6). Next, I refer to models and robots based on insect walking and phonotaxis (section 2.7). Finally, I conclude this chapter by summarising the open questions derived from the current literature (section 2.8).

2.2 Cricket Behavioural Ecology

Crickets belong to the order of Orthopteran insects, which also encompasses katydids, grasshoppers and locusts. There are more than 2600 species, many of them nocturnal, living in a variety of habitats (Walker and Masaki, 1989). For instance, field crickets live on the ground, under rocks and burrows and mole crickets live underground in

tunnels that they construct. In contrast to locusts they prefer to walk rather than jump and despite the fact that they have wings, most of them are not able to fly.

Many species of Orthoptera, including crickets, have the ability to generate sounds by rubbing together certain hard body parts. This process of sound production is termed stridulation. Male crickets produce sounds by rubbing their two forewings which contain rows of corrugated bumps. Only few cricket species have been investigated in depth. Most of them belong to the families of field crickets, bush crickets and mole crickets.

Adult females of the species *Gryllus bimacullatus* (de Geer), which belongs to the family of the field crickets, will be used in this study. *Gryllus bimacullatus*, from now on referred to simply as the cricket, unless otherwise specified, has been the subject of numerous behavioural and neural studies related to auditory communication (Popov and Shuvalov, 1977; Popov et al., 1978; Selverston et al., 1985; Huber and Thorson, 1985; Stabel et al., 1989; Wendler, 1990; Michelsen et al., 1994; Poulet and Hedwig, 2005). There is also a significant amount of literature regarding behavioural and neural data associated with walking (Laurent and Richard, 1986a,b; Böhm and Schildberger, 1992; Nishino, 2003; Witney and Hedwig, 2011), making this species a suitable organism to investigate the auditory and walking behaviour interaction.

2.2.1 Phonotaxis

Taxis is a behaviour that involves the responsive movement of an organism towards or away from an external stimulus source (Fraenkel and Gunn, 1940). Organisms that have a paired set of sensors and move towards the most strongly stimulated side produce positive taxis. If they turn towards the less stimulated sensor they produce negative taxis. Organisms that have only one sensor, can still produce taxes by turning left and right and measuring the different stimulus intensities. Taxes depend on a frequent signal from the stimulus source, but they are robust compared to accurately identifying the source and planning a path towards or away from it and also can deal with changes in the position and orientation of the source. Examples of taxes include phototaxis which involves movement in response to light stimulation, chemotaxis which involves movement in response to chemical stimulation and thermotaxis which involves movement in reponse to temprerature gradient.

The ability of an organism to approach a sound source is called positive phonotaxis or simply phonotaxis. Female crickets approach to the male calling song is one of the

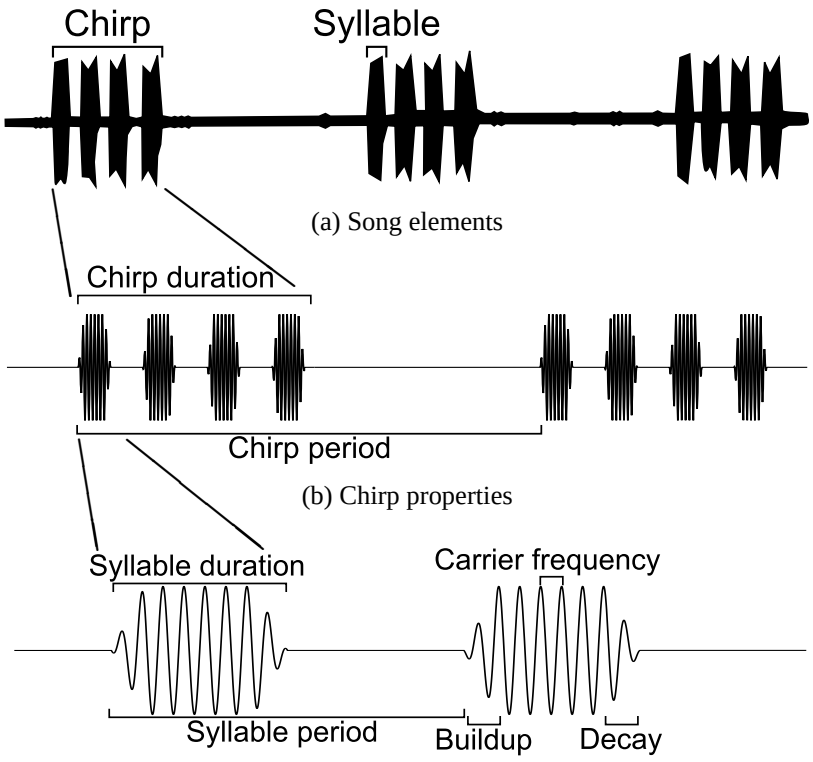
most well studied behaviours in acoustic communication and it requires pattern recognition and sound localisation. Many studies have focused on aspects of this behaviour. For example, the nervous system's generation and control of the song (Kutsch and Huber, 1989), the physics of sound production (Bennet-Clark, 1989) and the tracking of the song by the female (Weber and Thorson, 1989).

2.2.2 Calling Song

Males of most species can produce more than one type of song. These are mainly the calling song, which is used to attract the females from a long distance, a courtship song which is used when the female is in a close proximity (when other kind of cues such as tactile, vision and chemosensory stimuli play an important role) and an aggressive song used to establish territory and signal possible combat with other males. The calling song is the most studied and the one of interest to this study.

A typical pattern of the calling song is illustrated in figure 2.1(a). It consists of short sound pulses called syllables (figure 2.1(c)). Each syllable is produced when the male closes its forewings, is around 16–20 ms long and has a frequency between 4.5–5.0 kHz. A group of syllables separated by a short pause is called a chirp (figure 2.1(b)). Every chirp contains 3–5 syllables and has 350-400 ms duration (Huber, 1960), although there are significant differences between individuals of about 100 ms (Doherty, 1985). The syllable repetition interval (SRI) within a chirp is around 45 ms (Doherty, 1985). A chirp that has no pauses between syllables and continues for a prolonged period is called a trill. Environmental factors such as temperature affect the production of sound and therefore properties of the song. The temperature for the aforementioned properties values was between 20-21°C. Doherty (1985) found that the syllable period and the chirp period are affected by temperature changes. In contrast, the number of syllables, the syllable period and the carrier frequency were relatively unaffected.

Crickets do not live isolated in their environments. Sounds from other insects and other species are present in their daily lives. In order to be able to successfully locate the males of their species, the females must recognise the unique properties of their calling song. Some of the parameters of the song are crucial for this process. The syllable period has been found to be the most important (Thorson et al., 1982). Other parameters such as the syllable duration, the chirp interval and the number of syllables contribute to the attractiveness of the song (Popov and Shuvalov, 1977; Doherty, 1985; Stout and McGhee, 1988).



(a) Song elements

(b) Chirp properties

(c) Syllable properties

Figure 2.1: Cricket song example with its elements and properties. (a) Calling song consists of syllables and chirps. (b) A chirp is composed by one or more syllables and is defined by its duration and period. (c) A syllable has certain carrier frequency and is defined by its duration and period.

2.3 Morphology

An adult cricket is between 25-30 mm in length. As in all insects, a sclerotized cover called the exoskeleton, supports the body by surrounding all the soft tissue. The cricket has a laterally compressed cylindrical body shape (figure 2.2), composed of three main sections: head, thorax and abdomen. The thorax consists of three regions: prothorax (front), mesothorax (middle) and metathorax (hind). Each of these parts has a pair of legs. The rear legs are much larger than the front and middle, allowing the insect to kick and jump. Despite their differences in size and function, each leg is composed of the five following segments: coxa, which is attached to the thorax, trochanter, femur, tibia and tarsus (figure2.3(a)). The femur is the largest segment in mass and length in any of the legs. The tarsus is further separated in several segments, connected by passive joints and a claw, which make it very flexible. It is used to grasp objects and provide feedback about ground contact.

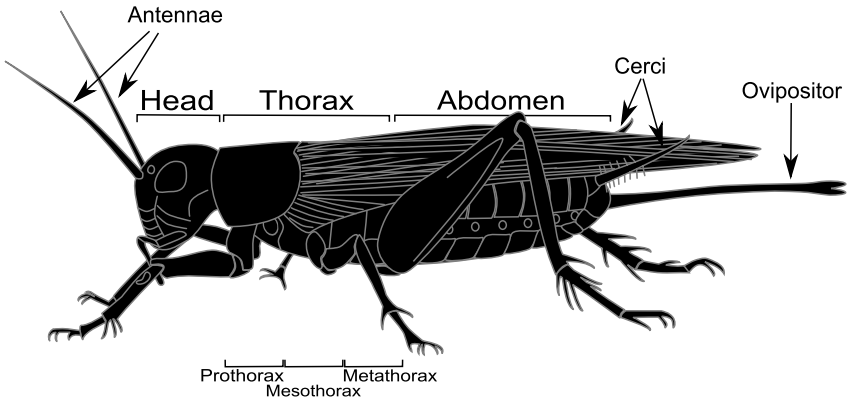


Figure 2.2: Schematic of a female cricket with main parts identified. Insects have sersors such as compound eyes, antennae and cerci to gather information from the environment. Additionally to the males, the females have an ovipositor to lay eggs in the soil.

2.3.1 Motor System

Each segment is moved by one or more pairs of antagonistic muscle groups, located in the previous leg segment (figure 2.3(c)). Every one of these muscles is attached on one side to a cuticular ingrowth (apodeme) and the other to the exoskeleton. The thoracocoxal (ThC) joint is a 3 degrees of freedom (DoF) connection, controlled by three pairs of muscle groups (promotor-remotor, abductor-reductor and anterior-posterior rotator). The front leg ThC joints have larger range of motion than the other regions, allowing the insect to perform actions such as cleaning the eyes and the antennae (Laurent and Richard, 1986a). The coxo-trochanteral (CTr - controlled by levator-depressor muscle groups), trochanteral-femoro (TrF), femoro-tibial (FTi - controlled by extensor-flexor muscle groups) and tibio-tarsal (TiTa) joints have 1 DOF each in every leg. As in most insects, the TrF joint has little movement and therefore coxo-trochanteral-femoro is considered as one joint. The coxal segments of the front legs are moving almost vertical relative to the ground, while the coxae of the hind legs are moving almost parallel to the ground and the coxae of the middle legs are moving somewhere in between (see figure 2.2).

2.3.2 Sensors

In order to monitor the state of their body and appendages and obtain information from their environment, insects have various types of mechanosensors. Positionally, they are distinguished into cuticular mechanoreceptors that are situated on the exosceleton

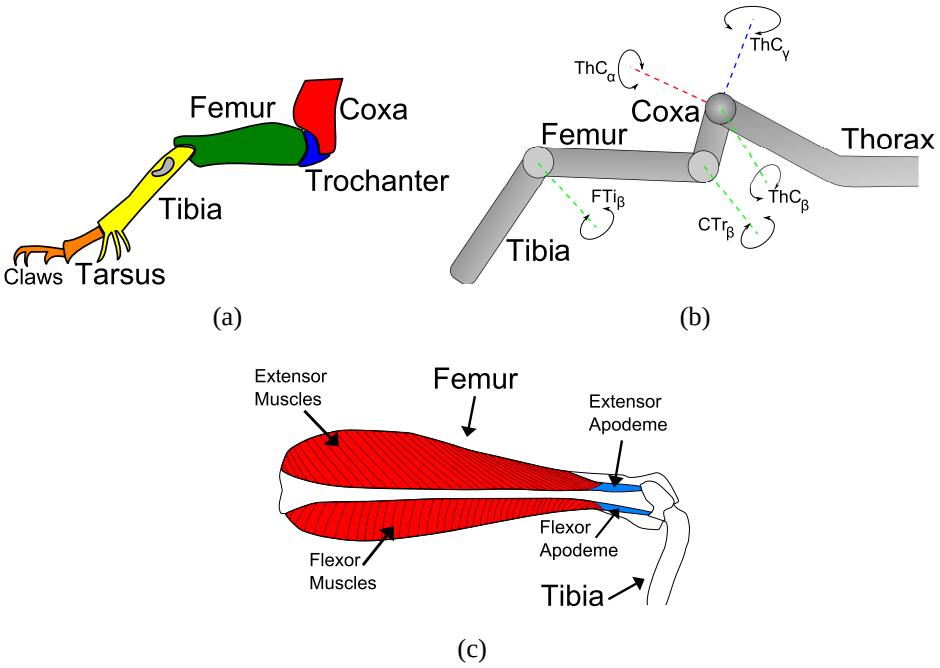


Figure 2.3: Properties of the cricket legs. (a) Front leg with segments identified. (b) Front leg with the main joints and their angular variables. The tarsus segments are not included. (c) Femur muscles and apodemes of the metathoracic leg.

and internal mechanoreceptors that are located inside the exosceleton, mostly near articulations. Functionally, they are separated into exteroceptors which are sensitive to outside stimuli such as air flow or touch and proprioceptors which respond to internal movements such as joint movement. The latter can be position sensors such as hair plates and chordotonal organs; and load sensors such as campaniform sensillae, strand and tension receptors.

2.3.2.1 Mechanosensors Involved in Walking

Various mechanosensors involved in walking have been identified in parts of the main body and legs of the crickets. One dorsal hair plate is located in each trochanter (Gnatzy and Hustert, 1989) and is used to estimate the angle between two joints. The chordotonal organs sense velocity, acceleration and position in each joint (stick insect; Hofmann et al., 1985). They have been studied for their neural morphology (Nishino and Sakai, 1997; Nishino, 2000) and function (*Acheta domesticus*; Nowel et al., 1995). In total 30 of them are located in the thorax. The campaniform sensilla measure the increase and decrease of the forces caused by the motion of the legs. There are 4-5 groups of them, in each Trochanter (Gnatzy and Hustert, 1989) and a group of 14-15

in each Tibia (Eibl, 1978). The strand receptors function quite similarly to the chordotonal organs. The tension receptors are located in some of the muscles and signal the force generated by the muscle. Crickets have also gravity receptors (Horn and Bischof, 1983; Horn and Föller, 1985). All these sensors can act in parallel and possibly influence each other (stick insect; Cruse et al., 1984). For a detailed table of sensor distribution in crickets see (Gnatzy and Hustert, 1989).

2.3.2.2 Auditory System

The ears are the most well studied sensors of the cricket. They evolved from proprioceptive chordotonal organs (Boyan, 1998) linked to a pair of tympanic membranes, on each foreleg, placed in the upper part of the tibia (figure 2.4(a)). Each pair consists of a large tympanum on the back of the leg and a smaller and less important tympanum on the front (Larsen, 1987). Tracheal tubes connect tympani to each other and to a pair of spiracles located in the front of the body, forming an H-shaped internal structure. A double central membrane separates the two sides (the medial septum). The lower branches of this structure end at the tympani and the upper branches end in the spiracles. For a complete description of the structure of those organs see (Ball et al., 1989).

The difference in the amplitude of the sound signal in the left and the right tympani is very low, because of the small distance of the ears ($\sim$1.5 cm) relative to the wavelength of the sound signal ($\sim$7 cm) and the distance of the sound source. Besides the direct route, where the sound waves reach each tympanum from the outside, there is a second indirect route thought the spiracles. As a result, the sound waves can pressure each tympanum both from inside and outside (Huber and Thorson, 1985), making the ear a pressure-difference receiver (Michelsen et al. 1994, Carew 2000, figure 2.4(b)). The two tympani will have a difference in the amplitude of their summed signals (from the four inputs), relative to the signal frequency, sound direction and diffraction. Consequently, the female, turns towards the side with the loudest sound and moves towards the sound source. For a detailed description of the sound perception in crickets see (Larsen et al., 1989).

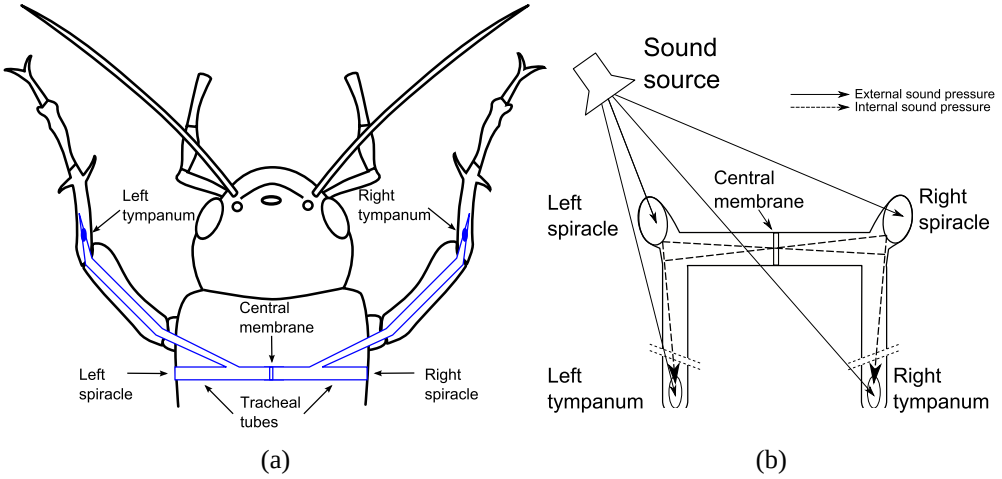


Figure 2.4: Auditory system of the cricket. (a) Position of the auditory system parts in the body. (b) Sound transmission through the tympani and the spiracles.

2.4 Experimental Strategies

Several experimental setups have been used, to study walking and phonotactic behaviour. They are different in the information they provide and the constraints they impose on the insect. Usually, a setup that has more constraints insect provides more information about the auditory input and the motor output.

2.4.1 Walking

Walking behaviour in the absence of sound stimulation in crickets has been studied using a treadmill (*Acheta domesticus*; Laksanacharoen et al., 2000) (figure 2.5(a)). The cricket walks on the transparent belt with a mirror at 45° below it, with small dots of paint applied at its leg joints and body on one side. This enables a simultaneous side and bottom view of the insect and the digitizing of the marked points, leading to a 3D reconstruction of the legs movements. Information about the angles of the joints were obtained by using inverse kinematics (Laksanacharoen et al., 2003). This setup allowed the kinematic analysis of straight walking but it cannot be used to study turning or a combination with sound stimulation. Another method is a narrow corridor with mirrors which was used to study the motion of *Gryllotalpa orientalis* (Zhang et al., 2011). This method has similar constraints to the treadmill. Also, because the insect is seen from the top and the side not all the joints are visible and therefore simplifications have to be made. An arena has been used as a less constrained setup, to study the forces generated by each leg but did not provide information about the movements of

each joint (Harris and Ghiradella, 1980).

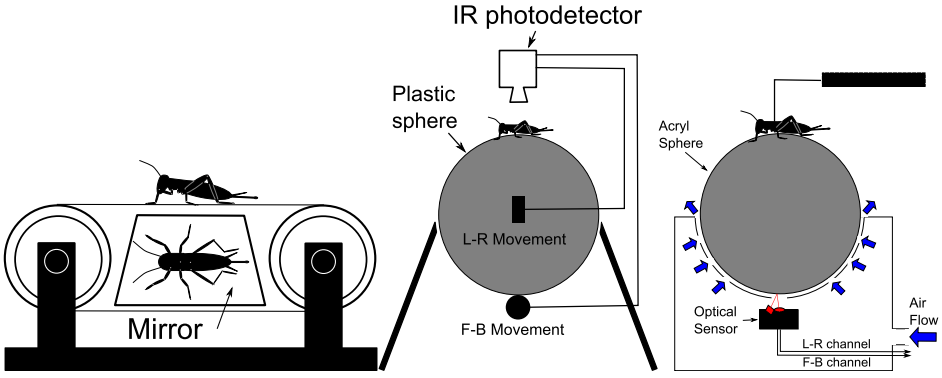
For other insects, data has been obtained for turning behaviours during free walking, *e.g.*, for ants (Zollikofer, 1994), bees (Zolotov et al., 1975), cockroaches (Franklin et al., 1981; Camhi and Levy, 1988; Jindrich and Full, 1999), flies (Strauss and Heisenberg, 1990; Mason et al., 2005), and stick insects (Cruse, 1976; Rosano and Webb, 2007). However, these generally report only the tarsus positions or foot-touchdown locations and the body orientation; in some cases forces exerted by the legs were also measured. More detailed three dimensional kinematic data has sometimes been obtained for free walking insects, *e.g.* for stick insects (Dürr, 2001) and cockroaches (Kram et al., 1997; Watson et al., 2002) but these are usually in situations where the animal is restricted from turning (the insect is walking on a beam or treadmill, or in a channel). These studies also required hand-digitisation to extract the joint positions from every frame. Joint angles have been estimated by using inverse kinematics calculations (Cruse and Bartling, 1995). Comparable kinematic detail that includes turning responses has otherwise been obtained only using animals that are restricted by tethering above a trackball or a slippery surface, *e.g.*, in beetles (Frantsevich and Mokrushov, 1980), cockroaches (Bell and Kramer, 1979; Nye and Ritzmann, 1992; Mu and Ritzmann, 2005; Ridgel et al., 2007; Bender et al., 2010), and stick insects (Dürr and Ebeling, 2005; Gruhn et al., 2009). In this type of study, some methods have been developed for at least partially automating the extraction of data from high speed videos. This usually involves marking of the joints, *e.g.*, with reflective paint (Larsen et al., 1995). Commercial motion capture systems such as WinAnalyze (Mikromak, Erlangen, Germany) have been used with such markers (Gruhn et al., 2006). Most recently Bender et al. (2010) have used image filtering and brightest point detection within a region near the expected marker location in an automated tracking algorithm to follow 26 marked points on cockroach legs, using two high-speed cameras to obtain three dimensional position data. A method that is widely used in human motion tracking is to constrain the tracking problem by defining a kinematic model that is fitted to the tracked points in the image (Aggarwal and Cai, 2002). This approach has been successfully applied to tracking a stick insect by Zakotnik et al. (2004). In fact, this approach is particularly appropriate, as instead of treating the the problem as one of tracking an arbitrary set of points (raw joint positions) in space, it assumes the points belong to a specific kind of articulated body. Indeed, the control problem for the insect is to use its muscles to change the angle(s) of each joint, in a coordinated fashion that propels it in a desired direction; thus to analyse the kinematics it is more useful to

know the angle than the position of each joint.

2.4.2 Phonotaxis

Field studies have rarely been used to investigate cricket phonotaxis, due to the difficulty of obtaining detailed and accurate data from an animal most active after dark and moving on the ground. Experiments including laboratory setups have been performed outside to take advantage of realistic environmental conditions (Römer, 1993; Kostarakos and Römer, 2010).

Various types of arenas have previously been used including rectangular arenas (*Scapsipedus marginatus*; Murphey and Zaretsky, 1972),(*Acheta domesticus*; Stout et al., 1983) a circular arena (*Teleogryllus oceanicus*; Bailey and Thomson, 1977), a Y-Maze (Rheinlaender and Blätgen, 1982), a Y-maze globe (Hoy and Paul, 1973) and a sound proof box (Payne, 2010). These setups can provide the path of the insect during phonotaxis, but it is not possible to determine the exact auditory input at a specific time. They are also useful in performing choice tests such as simultaneously presenting two songs and check the cricket's preference (Popov and Shuvalov, 1977; Pollack and Hoy, 1979). It is also possible to extract information about the orientation and speed of the insects (*Scapsipedus marginatus*; Murphey and Zaretsky 1972, *Teleogryllus oceanicus*; Bailey and Thomson 1977, *Plebeiogryllus guttiventris*; Mhatre and Balakrishnan 2007).



(a) Transparent treadmill (b) Kramer treadmill (c) Trackball

Figure 2.5: Three common experimental setups.

Setups that provide more information require that the insect is more restricted such as a Kramer treadmill (Weber et al., 1981) (figure 2.5(b)), a paired tread wheel (Stabel et al., 1989) and a trackball (Baden and Hedwig, 2008) (figure 2.5(c)). In the Kramer

treadmill the cricket is placed on top of a plastic sphere, with a small disk of reflective foil attached to her back. An infrared photodetector from the top senses the location of the insect and corrects the forward-backward and left-right position of the sphere, placing the cricket on the top. Although this setup does not recreate the exact conditions of the insect's natural environment, it allows the reconstruction of the insect path as if it had walked on the ground. In the trackball setup the cricket is attached by a restraining arm, which holds it on the top of an air-suspended sphere. An optical sensor then detects the left-right and forward-backward movements of the ball. This setup allows the measurement of the insect turning tendencies and has much faster time resolution than the Kramer treadmill. More recently it was used to obtain information of tarsi, head and abdomen positions (Witney and Hedwig, 2011). Some of these methods impose constraints on the insect movement which may make either tracking or interpretation of body and leg positions difficult. For instance, the insect's dynamics are altered if it is fixed on top of a trackball: propelling its own weight forward is not equivalent to propelling a ball backward (Poulet and Hedwig, 2005). Additionally, the spatial relation of the insect to external stimuli is held constant, which, whilst' providing suitable experimental control, does not reflect the normal phonotaxis situation. Some leg segments may not be visible from the available views of an animal on a trackball.

2.5 Behavioural Studies

2.5.1 Walking

Walking behaviour in insects has been mostly studied for the cockroach (Tryba and Ritzmann, 2000), the stick insect (Cruse, 1976; Epstein and Graham, 1983; Bässler and Büschges, 1998) and the locust (Burrows, 1996b). Walking is a task that requires for its maintenance translation of parameters, such as direction and velocity into actions and overcoming or avoiding obstacles. Typically, the control of walking in insects can be divided in two main tasks: The control of the movement of the single leg and the coordination of all the legs.

In order to produce successful movements, each joint in every leg, has to be in harmony with the movement of the other joints in the same leg. For the crickets, the ThC and CTr joints mainly determine the mobility of the whole leg and the amplitude of the step, while the FTi and TiTa joints allow an increase of the arc determined by the tarsus (Laurent and Richard, 1986a). As a result of the differences in the morphology

of the crickets legs, in each pair of legs the segments are moved in a different way than the others.

Thoracic differences have been noted in other insects (cockroach; Watson and Ritzmann, 1997), (locust; Burns, 1973). The stepping cycle of the single leg consists of two phases: stance (power stroke) and swing (return stroke) (figure 2.6(a)). Stance is the phase when the leg is touching the ground, supports the body and pushes it forward. Swing is the phase when the leg is lifted off the ground and moves forward until it reaches a reliable foothold on the ground. These two phases have major differences in their control requirements. During swing the leg does not require mechanical coupling with the other legs until it reaches the ground and therefore control is simpler, while in stance there is mutual mechanical coupling through the ground with the other legs, so as to support the body. Consequently, the transition events between the two phases are critical for the successful movement of the leg. The anterior extreme position (AEP) is where the leg touches the ground and the posterior extreme position (PEP) is where the leg lifts off the ground. The two phases and critical positions have been extensively studied for the stick insect (Cruse, 1985a,b).

The coordination of all six legs is essential for the successful movement of the body. Therefore, each one of them needs to communicate with at minimum the neighbouring ipsilateral and contralateral legs, so that they produce a stable gait. To have a statically stable gait, the centre of mass (CoM) must be within the polygon spanned by the legs on the ground (figure 2.6(b)). If the CoM projects outside of the stability polygon, the body is pulled by gravity and the insect falls. Insects typically walk utilising a tripod (used for high speed, with three legs touching the ground) or metachronal (used for slow speed and at least four legs touch the ground) gait (figure 2.6(c)). In the tripod gait, the front and rear leg of one side and the middle leg of the other side, perform their swing movements at the same time, while the other three legs support the animal. In the metachronal gait there is a sequence of stance-swing transitions on ipsilateral legs that is not in phase with contralateral legs. Cockroaches exhibit different walking speeds: A slow speed($<$10 cm/sec) and a faster ($\sim$30 cm/sec) when tested on an arena (Bender et al., 2011). According to Harris and Ghiradella (1980) crickets of the species *Acheta domesticus*, have gaits similar to cockroaches, with tripod gaits at high speeds and metachronal gaits at lower speeds.

Insects can turn in various degrees (cockroach; Comer and Dowd, 1987), on the spot (Simmons, 1990), while walking (cockroach; Watson and Ritzmann, 1997) or while running (cockroach; Jindrich and Full, 1999). During walking, turning can be

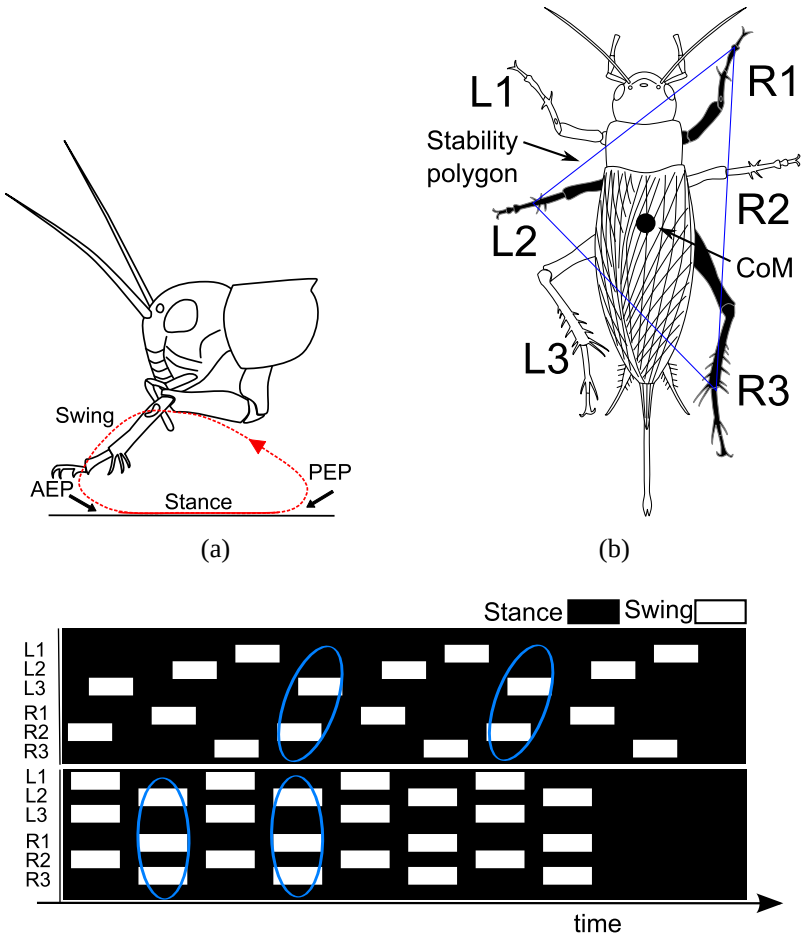


Figure 2.6: Illustrations of typical leg step, stability and gaits. (a) The stepping cycle is divided in stance or power stroke (solid line) and swing or return stoke (dashed line). The transitions between the two phases are the anterior extreme position (AEP) and the posterior extreme position (PEP). The arrow shows the direction of the leg during the stepping cycle. (b) The black legs are touching the ground, forming a stability polygon (in this case a triangle), while the white legs are moving forward. The centre of mass is located between the middle and hind legs. When it is within the stability polygon the insect is statically stable. (c) In the metachronal gait at least four legs are on the ground at any time and diagonal pair of legs are stepping approximately together (marked with an ellipse). In the tripod gait the front and rear legs on one side and the middle leg on the other side are stepping together. The black marks indicate the swing phase and the white the stance phase.

achieved by increasing step frequency (Graham, 1972) or step length (Strauss and Heisenberg, 1990). The initiation of turning in insects can be activated by brain neu-

rons (Ridgel et al., 2007) or reflex pathways that bypass the brain (Camhi and Johnson, 1999).

The small size of the leg segments makes it extremely difficult to study all the degrees of freedom in insects. Consequently most experiments focus on three DoF. The ThC which moves the leg forward and backwards, the CTr which moves the femur up and down and the FTi which moves the tibia closer or further from the femur. Laksanacharoen et al. (2000) analysed the forward walking on a treadmill of *Acheta domesticus*. In this research the complex movement of the coxae was determined for all the thoracic segments, indicating that only the front ThC joints use more than 1 DoF. There are obvious differences in the movements of the legs that belong to different thoracic segments. For instance the hind legs move almost vertical relative to the ground, while the front legs extend far forward.

2.5.2 Walking During Phonotaxis

Crickets approach the sound source in a series of consecutive runs and pauses following a meandering path (Weber and Thorson, 1989). The existing knowledge on phonotactic walking involves mostly turning tendencies measurements, such as direction, pathway and translational and rotational velocity (Weber et al., 1981; Schildberger, 1988; Stabel et al., 1989; Doherty, 1991).

Murphey and Zaretsky (1972) found that there is a correlation between the walking bouts and the stops in *Scapsipedus marginatus*. This however might be because the calling song of this species occurs less that one per second. Instead, *Gryllus campestris* had number of stops independent of the presence of the calling song (Schmitz et al., 1982). Earlier studies suggested that turns are followed by a stop and that the rest of the walking is not affected by the sound direction (Murphey and Zaretsky *Scapsipedus marginatus*; 1972, Bailey and Thomson *Teleogryllus oceanicus*; 1977). More recent studies on different species suggest that changes in walking angles occur during walking (*Plebeiogryllus guttiventris*; Mhatre and Balakrishnan, 2007).

Earlier experiments on a Kramer treadmill showed that the crickets were deviating by 30°-60° with respect to the animal's frontal midline. Recently, the accuracy of the directionality of the cricket was tested with the sound source present $\pm 30^\circ$ in front of the insect (Schöneich and Hedwig, 2010). It was found that it could move towards the correct direction even if the sound was placed 1° relative to the cricket's length axis.

Hedwig and Poulet (2004), using a highly sensitive trackball system, were able to

measure more precisely the movements of the females. The results showed that they make rapid steering movements in response to each sound pulse of a communication signal, independent of the species specific song. This observation indicates that phonotactic turning is initiated by a combination of reactive movements and brain neurons commands. Furthermore, Baden and Hedwig (2008) recorded the movements of the front legs using the same experimental setup. The up-down movements of the leg were not altered by the sound direction. In contrast, the left-right movements were clearly dependent on the sound direction, making larger movements towards the contralateral speaker and smaller towards the ipsilateral speaker.

Witney and Hedwig (2011) used one camera to record cricket movements from the top using the same experimental setup. This provided mainly information about the foot positions of each leg but due to the setup limitations I discussed previously, this did not allow precise information about each joint contribution and especially the ThC joints. The front and middle legs on both sides adjusted their movements during turning, but the altering of the hind legs' movements was small compared to forward walking.

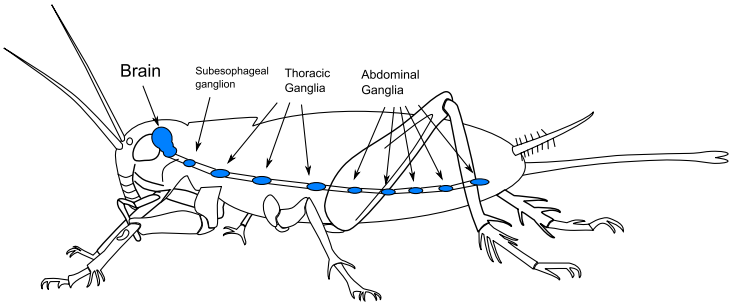
2.6 Neurophysiology

In the next paragraphs, I present the different groups of neurons that participate in the phonotactic turning behaviour and their contribution. The summary begins with the overall structure of the nervous system and continues with the local and ascending thoracic auditory neurons, the local brain neurons, the descending brain neurons and the motor neurons and the walking interneurons. The terminology for the neurons presented herein is not uniform, so I will include the names given by the authors in the citations.

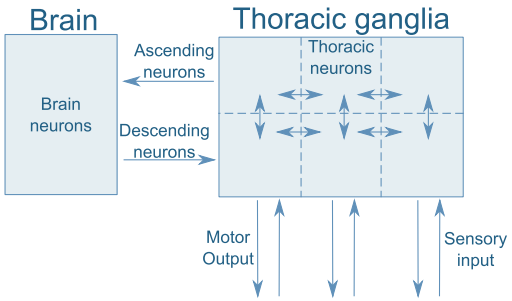
2.6.1 Nervous System

The central nervous system (CNS) of insects is composed of a series of ganglia (a collection of neurons), which are linked by intersegmental connectives, allowing signals to travel up and down this chain (figure 2.7(a)). The front ganglion is the brain, followed by the subesophageal ganglion, three thoracic ganglia and finally several abdominal ganglia. The highest concentration of neurons is located in the brain ($\sim$300K neuron cells in crickets (Schildberger et al., 1989), 100 times greater than any of the other

ganglia), which is responsible for learning (Matsumoto and Mizunami, 2002), processing of visual, olfactory (Schildberger, 1984a) and antennal (Gebhardt and Honegger, 2001) input and the overall control of the behaviours. The role of the subesophageal ganglion in locomotion is unclear, although evidence suggests it participates in maintaining normal walking (Altman and Kien, 1987). A thoracic ganglion is located in each one of the pro-, meso- and meta- thoracic segments and controls the muscles of the front, middle and hind legs respectively, as well as processing sensory input from these segments including auditory.



(a)



(b)

Figure 2.7: Nervous system and neural pathways. (a) Position of the ganglia in the cricket body. (b) Basic information flow between different regions of the body.

2.6.2 Local and Ascending Thoracic Auditory Neurons

There are ∼60 primary auditory afferents in each auditory organ (Michel, 1974). Their axons project to the auditory neuropil in the prothoracic ganglion (Eibl, 1978), transmitting information to local and ascending thoracic interneurons. Two pairs of ascending auditory neurons are well characterized (*Gryllus campestris*, AN1 AN2; Wohlers and Huber, 1982), (HF_1AN; Popov and Markovich, 1982), (Schildberger, 1988; Schildberger and Hörner, 1988), (Hennig, 1988, *Teleogryllus commodus*; STU, LAU), (Stabel et al., 1989), (TH1-AC1, TH1-AC2 Zorovic and Hedwig, 2011). Each AN1 receives

excitatory input from the ear contralateral to the cell body (Horseman and Huber, 1994). The AN1 pair is tuned to the calling song frequency and its hyperpolarization leads to the change of walking direction. Each AN2 receives input from both ears. The AN2 pair responds to higher frequencies and evidence suggest that is involved in bat avoidance (Schildberger, 1984b). Other identified neurons in the prothoracic ganglion in different cricket species are the descending neuron DN1 which receives excitatory input from the contralateral ear and responds to the calling song like AN1 neurons; and a T-shaped neuron TN1 which receives excitatory input from both ears (Wohlers and Huber, 1982, *Gryllus campestris*). However, the functional role of these neurons during phonotaxis is not clearly characterized.

All the identified auditory cell types in the thorax have their bodies located within the ganglion and each cell type has a mirror image (Wohlers and Huber, 1978). There are two well known bilateral pairs of mutually inhibitory omega neurons (Selverston et al., 1985), participating in phonotactic behaviour (*Teleogryllus Oceanicus*, Interneurons 1 and 2; Casaday and Hoy, 1977), (Wohlers and Huber, 1982, *Gryllus campestris*, ON1 ON2;), (LSAN; Popov and Markovich, 1982), (Wiese, 1981). ON1 is sharply tuned to the frequency of the song. Some studies suggest that these neurons do not participate in the temporal filtering of the song pattern (Wohlers and Huber, 1982; Schildberger et al., 1989), while others had evidence for low-level temporal filtering (Wiese and Eilts, 1985; Stabel et al., 1989). More recently, (Nabatiyan et al., 2003; Baden and Hedwig, 2007), it was proposed that the ON1 acts as a low-pass filter for the syllable patterns and that its instantaneous spike rate matches the tuning of phonotactic behaviour. Furthermore, the sound localization is activated independent of pattern recognition. Therefore, the pattern recognition is not directly involved in the rapid steering responses (Poulet and Hedwig, 2005).

2.6.3 Local Brain Neurons

Some local brain neurons have been associated with the recognition of the calling song. Schildberger identified two neuron classes with auditory responses (Schildberger, 1984b). The first, BNC1 gets direct input from the thoracic AN1 neurons (examined in the next section). Then it provides input to the second class the BNC2. The neurons belonging to both classes have different responses to the pattern of sound, acting as low- and high- pass filters. Similar neurons have been identified in other studies (UABN, PABN1, PABN2; Boyan, 1980), (*Acheta domesticus*, HBB1; Atkins

et al., 1988). Additionally, Böhm and Schildberger (1992) mention one local neuron that responded to the calling song with a latency of 25-30ms, but they do not clarify if it is one of the already identified neurons. This neuron acted differently in the standing and walking animal. When standing, often only the first syllable elicited spikes, while in walking there was a response to each syllable.

Schildberger's theory that high and low pass filtering result in band pass selectivity for syllable rate remains the most popularly accepted model for the recognition of the calling song. Other theories have been proposed that involve template matching (Hoy, 1978) or cross correlation analysis (*Teleogryllus*; Hennig, 2003). However, Hedwig (2006) suggests that these models require at least two pulses of the song syllables to produce turning. This fact indicates that these models are valid as a recognition mechanism but are too slow to be directly involved with phonotactic steering.

2.6.4 Descending Brain Neurons

The contribution of the brain to the walking behaviour through descending neurons is not entirely clear. Decapitated insects respond to external stimulation, but do not produce the same coordinated movements as they normally do (Zill, 1986, cockroach;). According to Staudacher (1998), there are about 200 pairs of descending neurons towards the thoracic motor centres. This number is small relatively to the total number of brain cells. The initiation of some behaviours has been associated with these neurons, for instance in cricket singing (Hedwig, 2000) and stridulation (grasshopper; Hedwig, 1994). For the walking behaviour, one pair of neurons was found (Böhm and Schildberger, 1992), that fitted the description of a command neuron. A command neuron can trigger a complex sequence of neural activity, such as stridulation or walking (Kupfermann and Weiss, 1978). The specific neuron had weak response to auditory, visual and tactile stimulation, but when walking began it increased its discharge rate. Additionally, when it was activated the cricket began walking during the discharge of the neuron.

Furthermore, there are some other descending neurons that have been associated with the walking and the phonotactic response. In older studies, groups of cells were active and directly correlated to a parameter of walking, such as translational (Böhm and Schildberger, 1992) and rotational (Staudacher and Schildberger, 1998) velocity. Moreover, in (Böhm and Schildberger, 1992) two neurons were found that responded to auditory stimulation. One of them was a unimodal neuron that exhibited sensitivity

to the direction of the sound. Besides sound stimulation, the other neuron responded to visual input. However this neuron only responded in the beginning of the calling song and almost stopped responding after a few chirps. Boyan and Williams (1981) found two neurons (IDBN and CDBN) that responded to auditory stimulation. The IDBN neuron is believed to belong to cluster i5 (Staudacher and Schildberger, 1998). Staudacher (2001) found that the majority of the descending neurons belonging to Group II had various responses to calling songs of 5 and 20 kHz.

Based on the above results from crickets and studies in locusts (Kien, 1983, 1990a,b), Heinrich (2002) proposed that the brain is not only responsible for the initiation and maintenance of walking, but there is a population of descending neurons controlling parameters of walking behaviour. Each neuron is responsible for a specific subtask, such as intra- and inter- leg coordination and contributes with fine tuned adjustments of walking patterns. This agrees with Baden and Hedwig (2008) who suggest that the steering commands are integrated with the networks that control for walking, by modulating the amplitude of the steering response.

2.6.5 Motor neurons and Walking Interneurons

The ganglia control leg muscles through excitatory and inhibitory motor neurons (Nishino, 2003), (locust; Watson et al., 1985; Siegler and Pousman, 1990), (cockroach; Cohen and Jacklet, 1967). The number of motor neurons in each ganglion is relatively small. For example, in the cricket prothorax, coxa, trochanter and femur in each leg are controlled by 50 motor neurons (1 unpaired and 49 paired) (Laurent and Richard, 1986a).

Each thoracic ganglion generates rhythmic motor patterns which alternate the contraction of antagonistic muscles, producing movements of the segments of the individual leg (locust; Ryckebusch and Laurent, 1993; Burrows, 1996a). The neural networks that generate these rhythmic patterns are described as “central pattern generators” (CPGs). Rhythmic motor patterns can be generated without sensory input (cockroach; Delcomyn, 1980). In stick insects, evidence suggest that they have separate pattern generator for each joint (Bässler, 1993; Büschges, 1995; Bässler and Büschges, 1998). The coordination of the leg joints is accomplished through interactions of the modules that control the joints. However, other results in the stick insects show that leg joints do not have strict coordinated motion (Cruse and Bartling, 1995), but are coupled by sensory information.

In insects, spiking and nonspiking interneurons are responsible for the control of

motor neurons. The difference between the two categories is that spiking neurons generate action potentials in order to transmit information (“digital” transmission), while nonspiking neurons function without generating action potentials (“analog” transmission). Spiking interneurons main role is to receive and distribute information from sensory neurons (stick insect; Hess and Büschges, 1999) and possibly contribute to the control of leg movement (locust; Wolf and Laurent, 1994). For instance, they process information from the femoral chordotonal organ (fCO) (stick insect; Büchges, 1994), (locust; Burrows, 1987). Instead, the nonspiking interneurons main responsibilities are to receive input from the spiking neurons, control the relevant motor neurons (cockroach; Pearson and Fourtner, 1975), (stick insect; Büsghes, 1990), (locust; Burrows, 1980; Laurent and Burrows, 1989), posture (locust; Siegler, 1981) and modulate the gain of leg reflexes (stick insect; Büschges et al., 1994). The sensory information plays a greater role in insects that move slowly (*i.e.* stick insect) than the ones that move in greater speeds (*i.e.* cockroach) (Delcomyn, 2004).

Besides the processing of information in each thoracic ganglion, the communication between the segments of the CNS is also important for the control of locomotion, through intersegmental interneurons (cockroach; Pearson and Iles, 1973). This communication is essential for the coordination of the movements of all the legs. The influences between ipsilateral legs are stronger than between contralateral legs (stick insect; Brunn and Dean, 1994). Additionally, the shared information between contralateral legs differs between the three thoracic ganglia (stick insect; Dean, 1989). Experiments in reduced leg preparations show that leg coordination is affected by the interaction of interleg and intraleg sensory feedback (Ludwar et al., 2005; Borgmann et al., 2007).

Baden and Hedwig (2008) performed recordings of the front legs tibial motor neurons activity during phonotaxis, revealing that the auditory input is indirectly integrated with the walking networks. There are currently two hypotheses for this connection. Either there are local thoracic interneurons connecting the thoracic auditory interneurons to motor neurons or that there is a connection through the ascending and descending brain neurons. Therefore, besides the modulation by the leg sensors, walking can be modulated by the auditory response.

2.7 Models and Robots

2.7.1 Walking

Most insect-inspired hexapod models are based on either the stick insect (*Carausius morosus*) or the cockroach (*Periplaneta americana*, *Blaberus discoidalis*). Therefore this section will contain more information about these insects and not crickets. There are two main categories of controllers: reflex-based and pattern-based. The former use the sensory input to produce leg movements and coordination, while the latter use pre-programmed patterns (mostly CPG), which might be modulated by sensor input.

As a result of extensive behavioural and neural experiments on stick insects, Cruse et al. (1991) proposed a set of rules for leg coordination (figure 2.8) and a "step pattern generator" for the single leg, capable of changing between stance and swing using load, position and velocity signals. The rules are the following:

1. The swing movement of a posterior leg inhibits the swing movement of an anterior leg.

2. The start of stance movement of a posterior leg excites the swing movement of an anterior leg.

3. A backward shift of an anterior leg's PEP will create an earlier swing movement and a forward shift of the posterior leg.

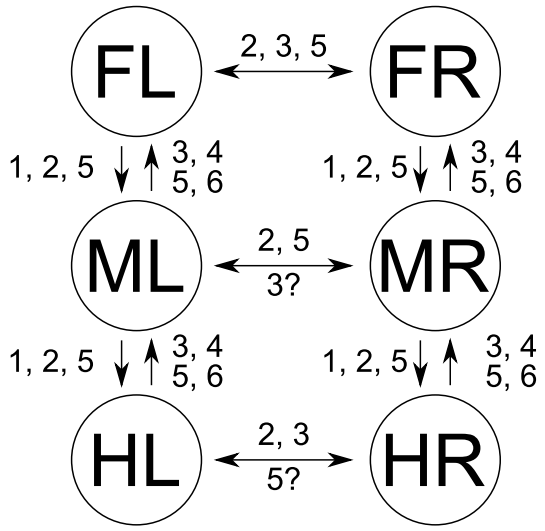
4. The posterior leg swing is targeted towards the position of the anterior leg.

5. Increased resistance increases force and increased load prolongs stance

6. The posterior leg will briefly step backwards when it treads on the anterior leg.

The proposed rules can be applied to forward walking situations. However, during crossing large gaps or turning the rules have to be adjusted (Bläsing and Cruse, 2004; Dürr, 2005). This model produced and maintained stick-insect-like tetrapod and tripod gaits in a simple kinematics simulation. A later version (Cruse et al., 1995), was based on a neural network architecture and transitioned between stance and swing using threshold values. The networks were trained with data from real insects. Cruse et al. (1998) proposed the successor of these models, WalkNet. This network consists of several subnetworks, of which the most important are the swing-net and the stance-net controlling swing and stance respectively and the selector-net which controls which

of the two networks is in control of the leg. There are three DoF per leg (α, β, γ). The network outputs velocities for each joint. A more recent version of the WalkNet model (Schilling et al., 2007) can function with leg amputations and the selector net is modified to accept an analogue signal for the load of the leg. This model has been tested in a dynamic simulation. Although these rules are based on stick insect locomotion, some of them or their variations could be applied to other insects since they have similar gait patterns. However, insects like cockroaches, locusts and crickets have also greater differences between the three leg pairs and higher speeds relative to the stick insect.



1. Return stroke inhibits start of return stroke
2. Start of power stroke excites start of return stroke
3. Caudal positions excite start of return stroke
4. Position influences position at end of return stroke ("targeting")

5a. Increased resistance increases force ("coactivation")

5b. Increased load plolongs power stroke

6. Treading-on-tarsus reflex

Figure 2.8: Cruse's rules that describe the information exchanged between neighbouring legs and the stance-swing transitions they generate.

A different solution regarding the control of stance in stick insects is the idea that the insect could use the elastic properties of each joint as a positive feedback (Bässler, 1988). Schneider et al. (2005) investigated this approach by using a local positive velocity feedback (LPVF) which can switch from positive feedback to compliant motion depending on the mechanical power produced by the joint (positive or negative). This model was tested on a two joint manipulator and a dynamic simulation of a leg Schneider et al. (2006). Rosano and Webb (2007) used LPVF principle in a model for turning, introducing the thoracic differences observed in the insect.

Although there are indications of central oscillators, even in each leg joint (Bässler, 1988), Walknet does not use any central oscillators to produce rhythmic motor output. Each bi-stable circuit flexes or extends the associated joint. Cruse (2002) proposed a simple network for the movement of each joint, where there are two antagonistic muscles channels of sensor input and motor output. Büschges et al. (1995) and Hess

and Büschges (1997) investigated which sensory signals could affect each of the three joint oscillators. This means that instead of using simple pattern generators, the joints movements are influenced by input from their neighbouring joints such as load and angle information. Akay et al. (2004) proposed a reflex chain for the generation of the forward stepping pattern of the middle leg, using three non-centrally coupled oscillators which are being coordinated by sensory signals. This model has been tested in a dynamic simulation (Ekeberg et al., 2004) and produced coordinated stepping movements of a middle leg and with some modifications the movements of a front and hind leg.

Some of the robots mentioned in the upcoming discussion have the primary goal of investigating biological systems, while others aim to improve robot performance. Since all the underlying mechanisms are not fully understood for any insect, neurological and physiological data are combined with engineering techniques for the construction of robots. Furthermore, the existing robot components are bigger, heavier, slower, have less power and consume a lot of energy. In contrast to the nervous system of an insect that does parallel computations, computers typically work serially. Consequently, the walking performance of robots is expected to be worse than the real insects.

Most hexapod robots, apart from the fact that they use legs, are not based on biological principles, *e.g.* Yoneda and Ota (2003); Barai and Nonami (2007). Furthermore, there are robots that are based on insect walking but do not use similar leg structure or maintain a mechanical coupling for the intra- and inter-leg coordination. Some examples include a cricket microrobot (Birch et al., 2000), RHex (Saranli et al., 2001), Whegs (Allen et al., 2003) and MechaRoach (Boggess et al., 2004).

Although WalkNet has only been tested in simulations, the decentralised architecture and some of Cruse's rules for leg coordination have been successfully implemented in robots with 3 DoF per leg (Espenschied et al., 1996; Lewinger and Quinn, 2008). The rules are used to adjust each leg's position at which is lifted off the ground (PEP) based on the positions of its neighbouring legs. When a leg reaches its PEP it is lifted off the ground and moves forward. When it reaches its AEP it moves down and returns to its stance phase. The PEP of each leg is calculated at each time step. There are three major mechanisms, that correspond to coordination rules 1, 2 and 5. The first mechanism makes a leg that is in swing phase preventing the other leg from swinging by repositioning backwards the PEP of that leg by a small value. The second mechanism makes a leg that just entered its stance phase encouraging the other leg to

enter its swing phase by moving the PEP of that leg forward by a small value. The third mechanism makes a leg that is in stance phase encourage the other leg to enter its swing phase by moving the PEP forward by an increasing value. A genetic algorithm (GA) is usually used for tuning the parameters of the coordination procedure.

The TUM robot (Weidemann et al., 1994) used a single leg controller (SLC) and a global leg coordination module (LCM), where each leg notified its neighbours of its state. A mathematical model (Weidemann et al., 1993), divided into four states based on state machines was used to control the individual leg. This robot was able to generate trajectories similar to the stick insect whilst avoiding obstacles. Tarry II used an inverse kinematics model to train a neural network to produce stepping patterns (Frik et al., 1998). Robot II was also able to create a continuous range of insect-like gaits (Espenschied et al., 1996). It was able to have reflexes such as searching for foothold, stepping reflexes, levator reflexes. Rough terrain navigation is accomplished by integrating insect-like reflexes with the gait controller. An elevator reflex is implemented to surmount large objects, and a searching reflex allows the robot to find a foot support on uneven or missing terrain. LAURON used a learning approach (Berns et al., 1994) with coordination signals such as velocity (Ilg and Berns, 1995) to perform insect gaits. A later version of this robot, LAURON III (Gassmann et al., 2001) used pre-calculated leg trajectories and replaced the coordination rules with a centralized architecture.

The development of stick-insect-inspired robots focuses on the leg movements and their coordination, while the cockroach-inspired robots aim towards the morphology of the insect and its speed. Robots such as sprawlita (Cham et al., 2002) do not have an insect-like structure but use kinematic features of a cockroach and incorporates the spring-loaded inverted pendulum leg movements of the insect into its walking, achieving great speeds. There are also robots the follow predefined trajectories based on kinematic data from the real insect such as protobot (Delcomyn and Nelson, 2000).

Quinn and colleagues have constructed a series of robots based on the cockroach. Initially they developed a distributed neural network (Beer et al., 1989) for the control of walking based on Pearson's pacemaker model (Pearson and Iles, 1973). Robot I (Beer et al., 1992) had 2 DoF on each leg and used this neural network as a controller. A CPG was used to generate the stance and swing transitions for each leg. It was able to walk in a straight line, on flat terrain and generate a range of cockroach gaits. Robot III (Quinn and Ritzmann, 1998) is a hexapod with kinematics based on studies of the *Blaberus discoidalis* (Watson and Ritzmann, 1997). It has a total of 24 degrees of freedom with 5 for each front leg, 4 for the middle legs and 3 for the rear legs moved

by air cylinders. The robot uses a distributed hierarchical controller. Robot IV used passive stiffness joints to store energy during a step cycle. Robot V (Choi et al., 2005) is able to control not only joint position, but also joint stiffness. These robots are able to imitate the cockroach posture but not to walk yet, as they are dependent on external power and air supply.

Some robots are great examples of incorporating the leg structure of real insects into a robot (cockroach; Delcomyn and Nelson, 2000; Choi et al., 2005), (stick insect; Pfeiffer et al., 1995). Despite the fact that the robots that use artificial muscles are closer to the biological muscles, they are difficult to control. Furthermore, they rely on external resources that complicates their performance.

Although robots such as TUM use a decentralised architecture for the coordination of their legs, each individual leg follows specific trajectories. Additionally, most of the aforementioned robots do not turn at all or they do not make turns similar to an insect. Finally, they do not implement the thoracic differences observed in the real insect.

Most robots use sensors related to walking, such as ground or load sensors, but do not use environmental sensors found on a real insect. For instance, Tarry II uses an ultrasound sensor for navigation. An antenna tactile sensor mounted on a robot (Cowan et al., 2005) is a good example of how turning is guided by external sensory cues. However, this sensor is mounted on a sprawl robot that cannot move the leg segments in the same manner as the cockroach.

Following the work of (Ekeberg et al., 2004), Lewinger et al. (2006) implemented the idea of sensory coupled oscillators on a single leg and two front legs. Additional sensory pathways for elevator reflex (step over a raised obstacle) and searching reflex (step over a gap) that are biologically plausible were added on a hexapod robot (Lewinger and Quinn, 2009). There is also a neural network implementation on another robotic platform that only deals with forward walking (von Twickel et al., 2011, 2012). More recently, a 4 DoF robotic leg based on cockroach middle leg could transition from forward walking to inside and outside turning by altering the sensory effect pathways (Rutter et al., 2011).

2.7.2 Phonotaxis

Webb and colleagues have developed successive robots which model the phonotactic behaviour of crickets, using Schildberger's (Schildberger, 1984b) low- and high- pass filter approach. The first model (Webb, 1995) was implemented on a LEGO robot. The

algorithm passes the auditory input from both sides through a phase cancelling process, lateralizing the sound of the species song frequency. Whenever the ear input value of one side reaches a threshold value, a turn in the appropriate direction is initiated. The first robot was only capable of reacting to slow syllable rates and therefore the model was transferred to a Khepera robot (Lund et al., 1997), capable of executing the model at cricket speed. The next model (Webb and Scutt, 2000) reimplemented the first model using spiking neurons. The most recent model (Reeve and Webb, 2003) approaches the internal structure of the insect neurophysiology, by including some of the identified auditory neurons (ON1, AN1, BNC1, BNC2) and the connections between them, as described in section 2.6. All the models were tested in a lab environment. The last model was used in outdoor experiments, using a Whegs robot (Horchler et al., 2004) with the ears mounted in the front part. Although the size of the robot prevented comparisons with the real crickets, it could reproduce the sound localisation of the insect when tested in a noisy environment, show preference for the species pattern of the song and distinct between competing sound sources.

In both robot implementations the distance between the two ears is fixed, while in the real cricket the distance between them relative to the ears changes while the insect moves. None of the aforementioned models has ever been tested on a multi-segmented legged robot, which could solve the Whegs sharp turns problem. Webb (2006) proposed a new modification to the current model inspired by the the more recent experiments on phonotaxis (Poulet and Hedwig, 2005). The key modification is a direct connection from the AN1 neurons to the motor control, which is modulated by the BN1 and BN2 neurons. This model has yet to be tested on a robot.

2.8 Open Questions

The current literature review reveals the lack of information in several aspects of the phonotactic behaviour and is summarized in the following questions:

From section 2.4:

- Can there be an alternative methodology to investigate the phonotactic behaviour, that allows detailed information about the body and leg movements of the cricket along with precise auditory input to be obtained while the insect is freely walking?

From section 2.5:

- What is the motion of each thoracic segment and body part during forward walking and turning?
- What is the motion of each individual leg joint during forward walking and turning?
- What are the similarities and differences with other insects?
- How do the legs coordinate during straight walking and turning?
- What is the speed of the cricket's response?
- Are the turns proportional to the sound direction?
- What is the accuracy of the sound tracking and what deviation causes corrections?

From section 2.6:

- What information might the cricket need to modulate its walking?
- What input might the motor neurons need?

From section 2.7:

- Does the cricket data resemble control mechanisms suggested for other insects for straight walking and turning?

In order to address these questions, I created a new methodology inspired by the limitations provided in section 2.4 and presented in the following chapter. The method will allow detailed data about the movements of a female cricket to be gathered while it performs phonotaxis. Further analysis presented in chapter 4, will allow the investigation of the remaining questions posed above.

Chapter 3

Methodology

N.B. The data presented in this chapter also appears in (Petrou and Webb, 2012).

3.1 Introduction

I concluded the previous chapter by indicating the open questions derived from the current literature. To address these questions I developed a method which is presented in this chapter. The overall aim of this method is to track the movements of a female cricket as it walks on a flat surface during orientation to sound under free walking conditions. It is necessary to film from underneath because all the joints are only visible from below the insect. Additionally, because of the insect's speed the videos need to be high-speed and two cameras have to be used that will allow 3D reconstruction of the joints. Finally, the information about the joint movements needs to be synchronized with the sound pattern.

The method I describe here generates joint angle data directly by incorporating an optimization algorithm which fits a kinematic model of the insect to the detected joint marker positions of each frame. This in turn supports more effective automation of tracking of the marker positions, building on the image processing methods described in Bradski and Kaehler (2008), Hedrick (2008) and Bender et al. (2010). This combination of methods enables tracking a cricket in a new experimental setup in which the animal can walk freely. The floor of the arena is transparent and thus I can film the animal from below, using two cameras to obtain three dimensional information about all leg joints. Instead of using a slippery surface, which alters the forces, or a treadmill in which the ground moves to keep the animal in the camera image, I instead move the cameras to follow the animal. The video is then processed offline by software that

automates the identification and tracking of joint markers, and reconstructs the motion. I demonstrate the system by tracking all leg joints and six body joints, synchronised with the sound pattern, for a cricket initiating a turn to sound from a standing start and walking towards it.

First I describe the materials and the methods used during the experiments including the arena, the preparation of the crickets, the experimental protocol and the acoustic stimulation (section 3.2). Then I present the software and its modules I developed to extract useful information from the video sequences (section 3.3). Finally, I present results from one experiment and evaluate the method (section 3.4).

3.2 Materials and methods

3.2.1 Arena

The setup (figure 3.1) consisted of a wooden (MDF) rectangular box with a transparent bottom made of acrylic plexiglass (3mm thick). The floor was slightly scratched with a knife providing friction while the insect walks on it, but preventing significant loss of image information during camera recordings. The walls and the ceiling were covered with a sound absorbent material (Audio 90/125 Illtec, Illsonic, Illbruck, Germany) to reduce sound reflections. Four fluorescent bulbs (75 W, Philips, Holland) provided the necessary light for the high speed recordings. I found that fluorescent light produces less flickering than ordinary bulbs, which is crucial for the tracking algorithms. Two speakers (Samsung SMS-2200), positioned on the left and right side of the box, were used to attract the insects, by alternately playing the calling song. The sound output was controlled by a custom made circuit equipped with a switch to change the direction of the song. In synchrony with the sound pattern this circuit flashed one of two LEDs, located under the arena and not visible to the animal, depending on the sound direction and status.

Two high speed colour cameras (Exilim EX-F1, Casio Co. Ltd., Tokyo, Japan; used with aperture 2.7, shutter speed 1/1000 s, ISO 1600, zoom 36 mm lens, focus (distance to animal) approximately 10 cm, resolution 512 X 384 pixels) were located under the plexiglass floor. Each imaged the same floor area of approximately 10 cm X 7 cm (a cricket covers an area around 4 X 2 cm) providing an effective resolution of about 5 pixels/mm, and capturing both the movements of the insect and the LED signal corresponding to the sound pulses. It was not possible with the cameras used

to obtain direct synchronisation between them, so the LED onset was also used to synchronise the cameras. Thus, recording at 300 fps , there could be a maximum difference of 3.33 ms between the left and right frames. In this worst case scenario, *i.e.*, the largest possible time gap between frames, I estimate from my data that the fastest moving point on the cricket (the hind leg tarsus during swing) would change position by no more than 1mm. I also verified that the potential delay does not add significant inaccuracy in practice by selecting marked points from the left frame and checking that the epipolar line in the right frame was over the corresponding point in the right frame. This was done after the calibration procedure described in section 3.3.1.

The relative position of the cameras was fixed using an aluminium triangle framework (35° degrees angle in the top of the triangle and 5 cm distance of the centre of the cameras lenses from the transparent floor). The framework was placed on two rails, one of them moving in the X-axis and the other in the Y-axis, and was moved by hand to maintain the insect near the centre of the images as it walked in the arena. The rails prevented rotation and translation around the Z-axis of the local coordinate system, which simplified subsequent analysis. They also constrained the motion to slow and steady movement—from the subsequent tracking I could calculate that movement of the cameras almost never exceeded 0.2 m/s which is the speed at which the image would be moved more than one pixel within one exposure at a shutter speed of 1/1000 s; consequently, this camera motion did not create significant blur. In order to construct the global arena position from the local image position I marked the floor with a grid of points, with 5 cm distance between neighbouring points. The points closest to the edge of the arena were marked with a number which indicates the global position of that point. Only one grid point is required for each frame to obtain the global position as further explained in section 3.3.4.

The cameras produce RGB video files compressed in H.264 format. These were first edited in Avidemux version 2.5 (http://fixounet.free.fr/avidemux/) to select the frames of interest: from when the insect starts moving until it hits the end of its tether (see below) and the camera is moved towards the edge to find the corresponding grid number. I also changed the video container (from QuickTime to AVI) and rotated the frames to represent left and right images for simplicity, before passing to the tracking software described in 3.3.

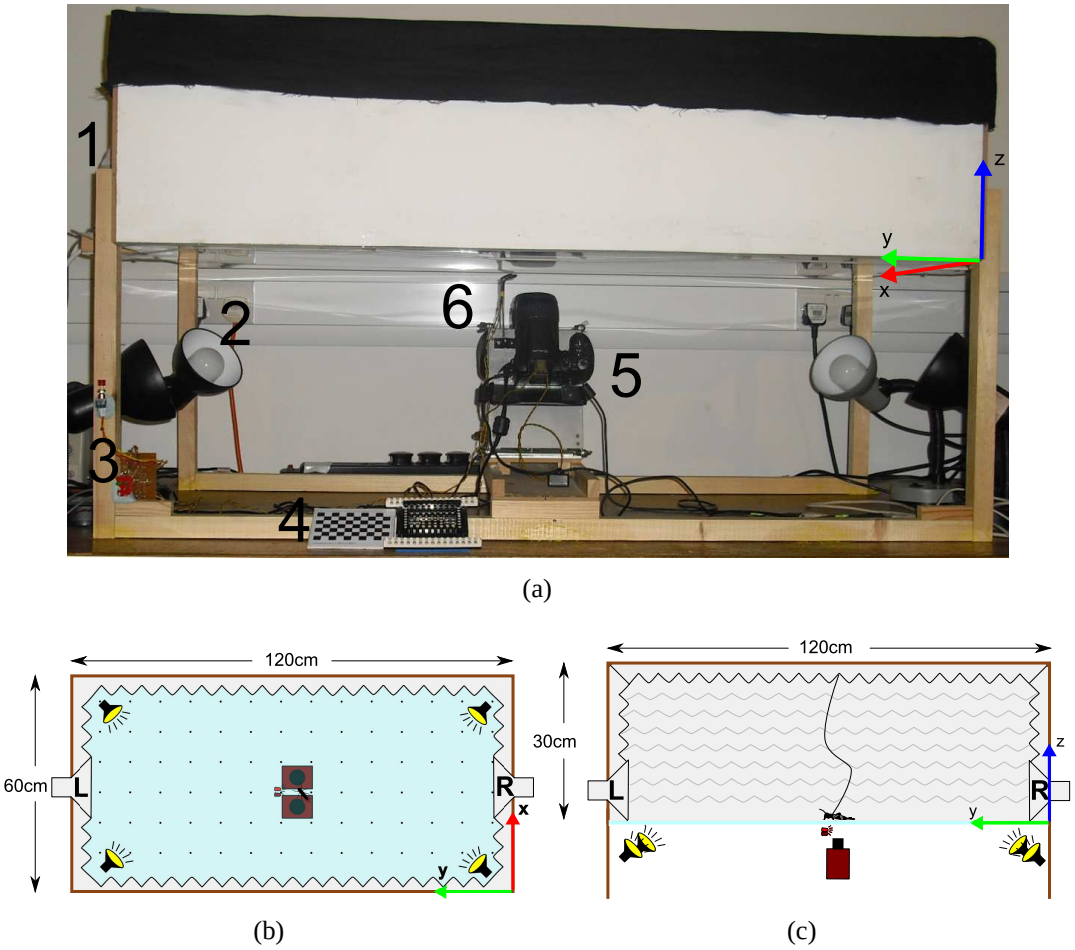


Figure 3.1: (a) The experimental setup with (b) top and (c) side schematics. Numbers in (a) indicate (1) The left speaker position. (2) One of the fluorescent bulbs. (3) The circuit and the switch that control the sound direction and LEDs. (4) Examples of planar and non planar calibration objects. (5) The stereo camera system. (6) The LEDs mounted on a thick metallic wire.

3.2.2 Animal Preparation and Experimental Protocol

Adult intact female crickets of the species *Gryllus bimaculatus* (de Geer) were obtained from a local supplier and separated into individual plastic cages, isolated from the sound of male crickets, before their final moult, maintained on a 12h:12h L:D photocycle and fed with dried dog food and water. Heat and light were provided by ordinary incandescent light bulbs. The experiments were performed at room temperature (20 - 24°C), and generally took place around the end of the light period or beginning of the dark period of the photocycle when the insect is most active (Loher et al., 1993). Their age was between one and four weeks after the final moult. Prior to experiments,

each insect was cold anaesthetized at 4-5°C for approximately 15 minutes and then placed on a block of Plasticine by restraining all legs with metal clamps. The two top wings were removed and a light string was attached to the insect's back, vertically relative to the body, at the third thoracic tergite using a mixture of wax and resin ($50\% - 50\%$). The string was used as a tether to keep the animal in a restricted area in the arena, so that it could not climb the walls. Small dots (approximately 1mm diameter) of yellow paint (TexPen, Dykem, KS, USA) were applied on the leg joints and at the centre of the thoracic segments.

The cricket was placed in the arena and the string attached to the centre of the arena ceiling. I gave the insect at least 1 hour to adjust to the new environment. A small twist applied to the string when attaching it meant that it acted as a very soft spring, adopting a helical shape to incorporate any additional length, and did not touch the ground or interfere with the animal's limbs. The recordings were started when the insect had paused for some time near the middle of the arena, where the string is not stretched and therefore did not affect its movements. In the example presented in section 3.4, the sound was switched on from one speaker, and the cricket's movements followed until it reached the limit of its tether, after walking about 35 centimetres. In most of my recorded paths the insect first rotated on the spot in order to orient itself relative to the sound source and then walked almost directly towards the speaker, usually without stopping.

3.2.3 Acoustic Stimulation

An artificial calling song was used, modelled on male *Gryllus bimaculatus* at carrier frequency of 4.8 kHz, syllable duration of 21 ms including 2 ms rise and fall time, syllable period of 42 ms, chirp duration of 252 ms and chirp period of 500 ms (Thorson et al., 1982), generated by a MATLAB 7.7 (Mathworks, Natick, MA, USA) script at 44.1 kHz sampling rate. The calling song was played back by using Audacity (http://audacity.sourceforge.net/) and presented by PC audio boards via the two active speakers. Sound intensities were calibrated to 75 ± 1 dB at the centre of the arena by using a sound level meter CEM DT-805 (Shenzhen Everbest Machinery Industry Company Ltd., Shenzhen, China) angled towards the active speaker.

3.3 Software

The nature of my method requires the processing of a few thousand frames per experiment. In order to avoid the manual digitization of multiple points in every frame, I developed software to assist me in my effort.

The software package called CricketTracker was developed in C++.NET, using Visual C++ Express (Microsoft, Redmond, WA). The package integrates a GUI with the OpenCV library version 2.2 (http://opencv.willowgarage.com), which I use for the video processing as it offers many built-in image processing functions that I use in my application. Most of the vision methods used in my system are described in Bradski and Kaehler (2008). Furthermore, the software utilizes basic OpenGL (http://www.opengl.org/) functions for depicting the 3D reconstruction of the tracked data. My software includes modules for camera calibration, kinematic model definition, tracking of marked joints, tracking of grid points, tracking sound status and direction, stance - swing transitions and playback. All the different modules of the software are explained in the following sections.

3.3.1 Calibration

The calibration module is used to calibrate the stereo camera system, using the StereoCalibrate algorithm in OpenCV. The calibration can use either a planar chessboard or a shape of known geometry and dimensions. In my case I used an object composed of LEGO^{TM}building blocks (Lego, Denmark) marked with 60 points as the calibration object. The average RMS reconstruction error was 0.3586 millimetres, and average RMS projection error 0.7856 pixels. Note this calibration takes into account camera distortion, by fitting a polynomial transformation, and therefore I can undistort the video frames. During video recordings, the insect is usually near the centre of the frames, but the grid points are sometimes near the edges where there is more distortion.

3.3.2 Kinematic Model (“Skeleton”)

In this module the user can define the kinematic model that will be used during the tracking procedure. This consists of a definition of the joints and the segments, the number of axes through which each segment can be rotated and thus the number of angles defined for each joint, and the minimum and maximum possible values for each of these angles (an angle can also be fixed at a constant value). The model has an

initial (root) point that defines the overall translation and rotation of the model relative to the axes origin, as it is fitted to the data. Limits for the permitted offset in x, y and z position of this initial point during the fitting procedure can also be specified; typically I used limits of ± 0.5 mm. The rotation order of the angles can also be selected here. In my case I used

$$R = R_y \times R_x \times R_z \tag{3.1}$$

The module saves the defined joint and segment information in XML files. An example of the two files with one element is provided in the next lines.

```
<?xml version="1.0" encoding="utf-8"?>
<Joints>
   <Joint Name="Middle Right Femur Tibia" IsRoot="False" IsLegRoot="False" />
</Joints>

<?xml version="1.0" encoding="utf-8"?>
<Segments RotationOrder="2" RootOffset="0.5" OppositeSegmentsSameLength="True">
  <Segment Name="Middle Left Tibia" FromJoint="8" ToJoint="9" OppositeSegment="4" HasAlpha="False"
   IsAlphaConstant="False" MinAlpha="-180" MaxAlpha="180" HasBeta="True" IsBetaConstant="False"
   MinBeta="0" MaxBeta="180" HasGamma="False" IsGammaConstant="False" MinGamma="-180" MaxGamma="180"/>
</Segments>
```

As an example, see figure 3.2(a), 3.2(b) and table 3.1 for the definition of the model used for tracking the cricket. Detailed anatomy of the cricket leg joints has not (to my knowledge) been published except for the proximal front leg joints (Laurent and Richard, 1986a); a much briefer description of the degrees of freedom (DoF) for all leg joints is given in (Laksanacharoen et al., 2000). My model was obtained by making reasonable assumptions based on these and other insect studies, and also by systematically exploring the effect on tracking accuracy of increasing or decreasing the DoF of various joints. A body model that lacks a true DOF of the cricket will produce greater fitting errors, whereas an unnecessary DOF in the model will not significantly improve the fitting errors, and can be discounted. For example, I found that including constant rotation in the trochanter-femur joint for the front legs (a similar rotation of the corresponding joint is assumed in recent cockroach studies Bender et al. (2010)) significantly improved the fit, but adding this rotation or a DoF to this joint in the other legs made little difference.

The model used consists of three central joints in the pro-, meso- and meta-thorax parts of the thorax. The root point of the translation and rotation of the kinematic model is set to the meta-thorax joint which is close to the centre of mass and provides better matching values during the tracking procedure than any other body joint. The meso-thorax is considered to have the same rotations as the meta-thorax, but the prothorax

has three DoF. The rest of the joints were introduced in chapter 2 in section 2.3.1. The TiTa joint is marked but the rotation of the tarsus is not estimated; and a single marker is tracked for the CTr and TrF joints, which jointly act to rotate the femur relative to the coxa. The front legs (figure 3.2(e)) have three DoF in the ThC joint (Laurent and Richard, 1986a), a one DoF hinge CTr joint, a constant 45° rotation of the TrF joint, and a one DoF hinge FTi joint. The middle legs (figure 3.2(d)) have three DoF in the ThC joint and one DoF hinge CTr and FTi joints; the TrF joint does not move. The hind legs (figure 3.2(c)) similarly have three DoF in the ThC joint, a one DoF hinge CTr joint and a one DoF hinge FTi joint.

Once the model has been defined, it needs to be initiated by the user manually selecting a point corresponding to each defined joint in the first frame of the tracking data, for each camera. The selected points are then triangulated, using the calibration information, to obtain the 3D positions. From this, the length of each segment can be calculated. If the user selects the appropriate option the length of each segment is derived by calculating the mean value of the left and right corresponding segments. For instance, the front coxa length (FC) is calculated by using the front left (FLC) and right (FRC) coxa length:

$$FC = (FLC + FRC)/2 \tag{3.2}$$

The symmetrical values are used because I assumed both sides have the same segment lengths and this simplifies subsequent analysis of the results. Alternatively the user can allow the model to remain asymmetric, *i.e.*, using the raw values for the FLC and FRC respectively. The initial values of the angles of the kinematic model are derived by taking the mean value of maximum and minimum permitted value for each angle (see table 3.1) which have been set to very generous values at the limits of plausible motion. For instance the average value of the front right FTi joint is derived by the type:

$$FRFTi = (MaxFTi + MinFTi)/2 \tag{3.3}$$

where $MaxFTi = 180^\circ$ and $MinFTi = 0^\circ$. An initialised model for the cricket is illustrated in figure 3.2b.

3.3.3 Tracker

The tracker uses constrained nonlinear optimisation to fit the kinematic model to the joint markers extracted from each image pair, where finding and identifying each joint marker is based on an image matching process that uses the joint positions estimated in the previous frame. The software interface is shown in figure 3.3. For convenience of explanation I will first describe the fitting procedure, assuming that a potential match for each joint has been extracted from the current images and triangulated to obtain an x,y,z position estimate. The aim is to find the optimal estimate of the model angles to minimise the deviation of the model joint positions from the image estimates, given the fixed distances between joints and limits of joint motion that has been set in the initialisation procedure described above.

I used an active set algorithm (ASA) for constrained nonlinear optimization as described in Hager and Zhang (2006) and implemented in the ALGLIB version 3.2 (http://www.alglib.net) library to minimize the euclidean distance between the joints of the kinematic model and the estimated positions from the images (Equation 3.4). Active set algorithms are a group of methods used to solve optimization problems with equality/inequality constraints. The name of the method is derived from the fact that at a current point each constraint is either active or inactive. The algorithm reduces the problem from an equality/inequality constrained problem to a sequence of equality only subproblems that can then be solved and used as the basis of an iterative process. During this procedure, the active constraints are treated as equality ones and the inactive are ignored. The algorithm utilizes a conjugate gradient method (Hestenes and Stiefel, 1952) internally for the optimization.

$$f(x) = \sum_{n=1}^{n} w_n \sum_{i=1}^{3} \|p_i - q_i\|^2 \tag{3.4}$$

where p_i is the position in the model, q_i the estimate, and w_n is the weight for each joint. The weights reflect the output of the matching algorithm, described further below, such that estimates based on good matches have a higher influence on the fitting procedure, and poor matches will have less effect.

Because the algorithm I use is not gradient-free I used a four point centre formula to estimate the gradient for every variable.

$$\nabla f(c) = (\frac{\partial f}{\partial q_1}(c), \ldots, \frac{\partial f}{\partial q_n}(c)) \tag{3.5}$$

$$\begin{aligned}\frac{\partial f}{\partial q_i}(c) = \quad & \frac{1}{12h}(f(q_1,\ldots,q_i-2h,\ldots,q_n) \\ & -8f(q_1,\ldots,q_i-h,\ldots,q_n) \\ & +8f(q_1,\ldots,q_i+h,\ldots,q_n) \\ & -f(q_1,\ldots,q_i+2h,\ldots,q_n))\end{aligned} \tag{3.6}$$

where c represents the kinematic model chain and $q_0, q_1, \ldots, q_n$ the parameters of the model and $h = 0.1$. Computation of the gradient value for every parameter takes place in a separate thread to increase speed.

For the first image pair, the estimated joint positions are simply those chosen by the user during the initialisation process (and all the weights are set equal to one). The initialised kinematic model (figure 3.2b) is optimally fitted to these estimates. The 3D model co-ordinates are then used to define the template image of 8 X 8 pixels and the search region for each joint marker in the next frame pair, by reprojecting their locations to each image, and defining a window of 20 x 20 pixels around them. A Kalman filter (Kalman, 1960) is also initialised and is used to predict the position of each marker in the next frame, assuming it maintains a constant velocity, in case a particular joint marker cannot be located in a particular image, which is usually the result of occlusion.

The marker is located within the window using either template matching by normalized cross correlation, or colour histograms (figure 3.4). I used the standard algorithms available in the OpenCV library (MatchTemplate with methods CV_TM_CCORR_NORMED and CalcBackProjectPatch; see http://opencv.itseez.com/). This provides both a location estimate and a value for the goodness of the match (values range between zero and one with the latter providing a perfect match). If this value is equal or greater than a threshold value (in my case 0.8), I have a positive match. The weight to be used in optimisation is then derived by dividing this marker's match value by the minimum template matching value of the current frame:

$$W_i = V_i / V_{min} \tag{3.7}$$

Additionally, the software can utilise image filters such as background subtraction, contrast and brightness adjustment, colour filtering, binary thresholding, and smoothing to enhance the matching procedure. The user can apply any of these filters by selecting them in a property grid. During tracking image filters are applied only within the search regions to reduce computational cost.

If a point is not positively located by the matching procedure, then the Kalman

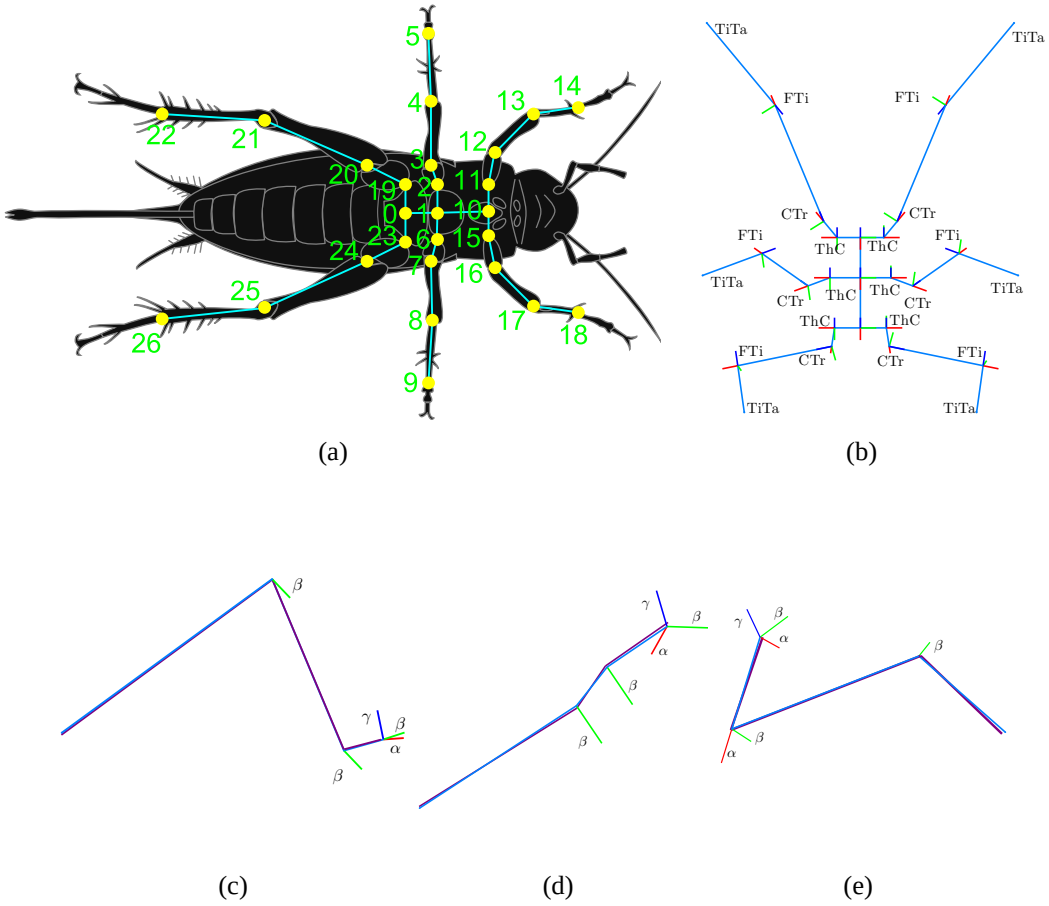
prediction is used to indicate the missed point if it falls within the search region. The weight value for the predicted point is equal to the value returned by the matching procedure (between 0.4 and 0.8). If the match value is below half of the matching threshold value (*i.e.*,in my case, 0.4), or the prediction of the Kalman filter falls outside the search region, the algorithm stops and the user needs to select the missed point from the current image. Typically the algorithm works uninterrupted (*i.e.* tracks all 27 points without violating the stopping criteria) for about 30-80 frames. The most common problem that stops the algorithm is the failure to track the front ThC joints. This happens because the front coxae are almost vertical relative to the body and thus tend to occlude the ThC joints.

Once estimates for the positions for all the joints are obtained in the current image pair, the kinematic model is fitted to the new data, as described above. Note that the starting point for the optimisation in this case will be the model parameters fitted to the previous frame. At high frame rates there should be minimal change in the angles, making this fitting procedure efficient.

The final output of the tracking procedure is the set of positions and angles for each joint for each frame in CSV (Comma Separated Values) file format. The software allows the user to choose to apply three different techniques for smoothing of the angles (cubic, hermite and penalized spline interpolation) as implemented in the ALGLIB library. It can also smooth the root joint location (in this case the metathorax joint) by using a moving average window formula used to reconstruct the translation (see subsection 3.3.7).

3.3.4 Grid

The Grid module is used to track the grid points on the ground, which provides a reference frame to locate the kinematic model in real space (see section 3.3.7). The user gives the initial global position of each point visible in the image (X,Y,Z coordinates, with the Z coordinate set to zero, *i.e.* the floor) and the range of frames that each point is tracked. The global positions can be extrapolated from the final frames of the sequence which always include an identified grid point on the edge of the arena (see section 3.2.1). The tracking algorithm used is the same as the tracker module, except in this case there is only one point tracked in each of the left and right frames. The grid coordinate positions are also smoothed by using a moving average window formula.



(a) (b) (c) (d) (e)

Figure 3.2: The kinematic model of the cricket. (a) The painted joints of the cricket's body and legs are indicated with yellow dots and the segments with cyan lines. See table 3.1 for corresponding joint definitions. (b) shows the model with the initial angles based on taking the midpoint of the defined limits of the angles for each segment. Each joint potentially has three axes of rotation: roll α around the X axis (red); pitch β around the Y axis (green); and yaw γ around the Z axis (blue). (c), (d), (e) show the joints of the right hind, middle and front leg of the fitted model in the tracked data for a frame. The purple lines indicate the tracked points and the blue lines the corresponding model. Each leg has 3 DOF at the thoraco-coxal joint, and one DoF (β) at the coxo-trochanteral and femoro-tibial joints; the front legs have an additional constant rotation (α) at the trochanter-femur joint (co-located with the coxo-trochanteral joint).

3.3.5 Sound

The sound module is used to determine the sound state (on or off) and direction (which end of the arena) by monitoring the LED indicators. In order to do that the user selects the area in the image corresponding to each LED and gives a threshold for the colour.

Joint	**Parameters**	**Limits**
Metathorax (0)	x, y, z	$[x_0 - 0.5\ x_0 + 0.5]$, $[y_0 - 0.5\ y_0 + 0.5]$, $[z_0 - 0.5\ z_0 + 0.5]$
Segment	**Parameters**	**Limits**
Metathorax - mesothorax (0 - 1)	α, β, γ	$[-30^\circ\ 30^\circ]$, $[-30^\circ\ 30^\circ]$, $[-180^\circ\ 180^\circ]$
Middle right coxa (2 - 3)	α, β, γ (ThC)	$[-90^\circ\ 90^\circ]$, $[-30^\circ\ 90^\circ]$, $[-90^\circ\ 90^\circ]$
Middle right femur (3 - 4)	β (CTr)	$[-180^\circ\ 0^\circ]$
Middle right tibia (4 - 5)	β (FTi)	$[0^\circ\ 180^\circ]$
Middle left coxa (6 - 7)	α, β, γ (ThC)	$[-90^\circ\ 90^\circ]$, $[-30^\circ\ 90^\circ]$, $[-90^\circ\ 90^\circ]$
Middle left femur (7 - 8)	β (CTr)	$[-180^\circ\ 0^\circ]$
Middle left tibia (8 - 9)	β (FTi)	$[0^\circ\ 180^\circ]$
Mesothorax - prothorax (1 - 10)	α, β, γ	$[-30^\circ\ 30^\circ]$, $[-30^\circ\ 30^\circ]$, $[-30^\circ\ 30^\circ]$
Front right coxa (11 - 12)	α, β, γ (ThC)	$[-90^\circ\ 90^\circ]$, $[-30^\circ\ 160^\circ]$, $[-90^\circ\ 90^\circ]$
Front right femur (12 - 13)	α (TrF), β (CTr)	45°, $[-180^\circ\ 0^\circ]$
Front right tibia (13 - 14)	β (FTi)	$[0^\circ\ 180^\circ]$
Front left coxa (15 - 16)	α, β, γ (ThC)	$[-90^\circ\ 90^\circ]$, $[-30^\circ\ 160^\circ]$, $[-90^\circ\ 90^\circ]$
Front left femur (16 - 17)	α (TrF), β (CTr)	-45°, $[-180^\circ\ 0^\circ]$
Front left tibia (17 - 18)	β (FTi)	$[0^\circ\ 180^\circ]$
Hind right coxa (19 - 20)	α, β, γ (ThC)	$[-90^\circ\ 90^\circ]$, $[-90^\circ\ 90^\circ]$, $[-120^\circ\ 0^\circ]$
Hind right femur (20 - 21)	β (CTr)	$[-180^\circ\ 0^\circ]$
Hind right tibia (21 - 22)	β (FTi)	$[0^\circ\ 180^\circ]$
Hind left coxa (23 - 24)	α, β, γ (ThC)	$[-90^\circ\ 90^\circ]$, $[-90^\circ\ 90^\circ]$, $[0^\circ\ 120^\circ]$
Hind left femur (24 - 25)	β (CTr)	$[-180^\circ\ 0^\circ]$
Hind left tibia (25 - 26)	β (FTi)	$[0^\circ\ 180^\circ]$

Table 3.1: The joints and segments of the model with parameters of the model and their limits. The units for the joint limits are in millimetres and for the angles in degrees. I used very generous limits due to the lack of prior information regarding the motion of the cricket. For instance all the FTi joints can rotate from -180° to -0° which leads to full flexion and extension of the tibia, which will never happen during the normal insect walking patterns.

When the LED is on this means that the colour is brighter and therefore the algorithm determines the sound as on. There is no significant delay between the sound output and the LED flashing as the circuit controls both outputs at the same time. Note, however, that as sound syllables are only 21 ms in duration, I may miss exact onset or offset by up to 3.33 ms due to frame rate. I can solve this problem by resampling the sound output as if it was every 1 ms and fitting the known pattern of the song by cross-correlating the two patterns. Note that the LEDs are attached to the triangular frame holding the cameras, and thus always stay in the same position in the image as the cameras are moved to follow the animal. Thus no additional tracking is required. However, the user needs to keep the camera frame positioned correctly around the animal to avoid overlapping of cricket appendages by the LEDs.

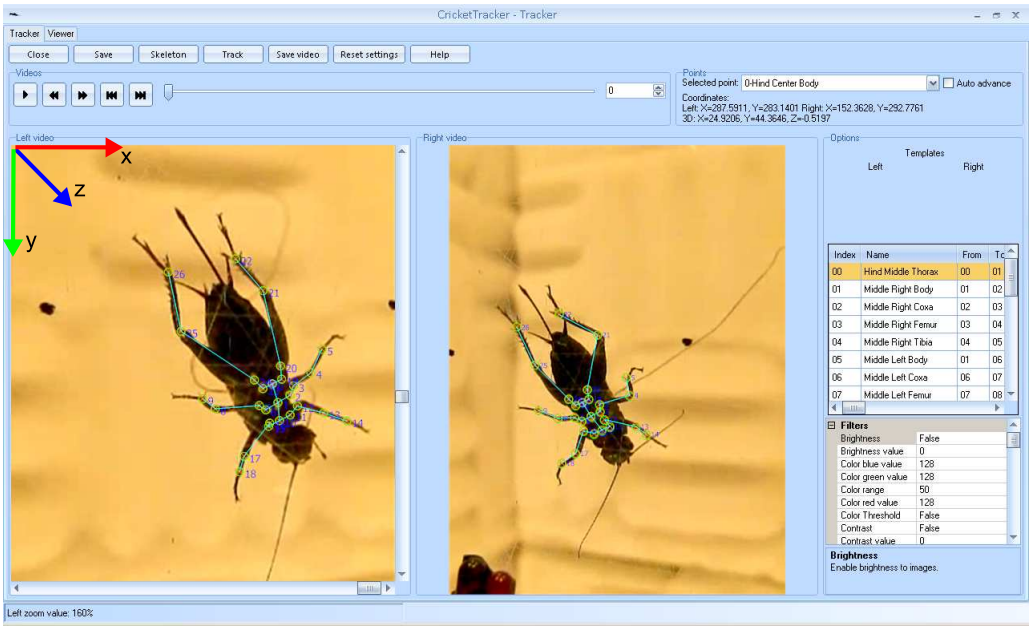


Figure 3.3: A screenshot of the tracker module of the software. The two images show the corresponding left and right frames containing the insect, the grid points and the LEDs in the bottom. The user can save the data, fit the kinematic model in the selected frame, begin tracking, save a video with the tracked points, reset settings and load the appropriate help file by pressing the top buttons. The viewer tab shows the tracked joints and segments in the OpenGL environment. The video buttons can be used to play the video or move to a certain position. The current joint can be selected from the combobox or by using the keyboard shortcuts. Information about the selected point coordinates are also displayed. Each frame can be panned or zoomed by using the mouse or the keyboard shortcuts. Undo-redo functions are also supported. Information about each segment such as the length can be seen in the middle right area. The settings for filtering the images and changing options for the algorithms and the appearance can be set in the property grid in the bottom right corner.

3.3.6 Stance-Swing

The stance - swing module is used to output the stance - swing state of each leg. The states for every leg can be determined by taking the Z coordinates of the TiTa joints from the tracker data, *i.e.*, swing is defined as whenever this joint has a Z value above a threshold. In practice, the threshold Z-value for swing needs to be set separately for each pair of legs (front, middle, or hind) due to the difference the leg geometries. Hind leg TiTa joints touch the ground in stance, while front and middle leg TiTa joints do not touch the ground. Typical values for the threshold were found experimentally (1.0 mm

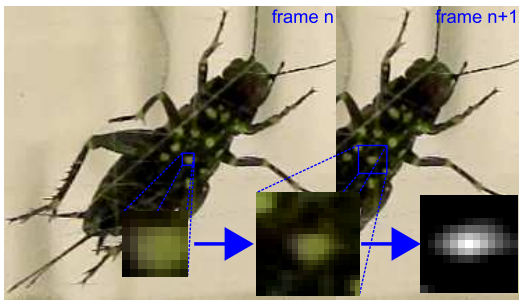


Figure 3.4: The procedure of tracking a point. The user selects the point in the frame n (first inset box) and the algorithm searches for the point in the region of the frame n+1 (second inset box). The best match is indicated by the brightest area (third inset box). Image filters have been removed for simplicity.

for the front and middle legs and 0.2 mm for the hind legs). The system also allows manual setting of stance state for each frame; this can be done before the tracking (*i.e.*, before coordinate information is available) or to correct any inconsistencies in the data that are observed by the user. The module visualizes the stance - swing states and the Z coordinates for every leg to ease this procedure.

3.3.7 Player

The player module (figure 3.5) combines all the information from the other modules to visualize the tracked cricket. First of all it calculates the difference of the tracked grid coordinates from the user defined coordinates given in the grid module (3.3.4). This gives the offset of the grid points and the cricket points.

To calculate the offset the following type is used:

$$T_{offset} = C_{real} - C_{gridPosition} \tag{3.8}$$

By using the above results I can calculate the global position of the cricket points by using the following type:

$$C_{global} = T_{offset} + C_{tracker} \tag{3.9}$$

This module can replay the motion of the cricket as it walks in the arena and observe from any angle. It can visualize the stance-swing transitions and the sound pattern. Furthermore, this module outputs the smoothed data (figure 3.11a) in CSV files for subsequent analysis. Also, resetting the translation and rotation of the metathorax to be zero reveals the relative motion of all the joints as if the insect had been fixed in

one position. This means the free walking data can be used for comparison with stationary setups such as a cricket on a trackball turning (figure 3.11b) or forward walking (figure 3.11c).

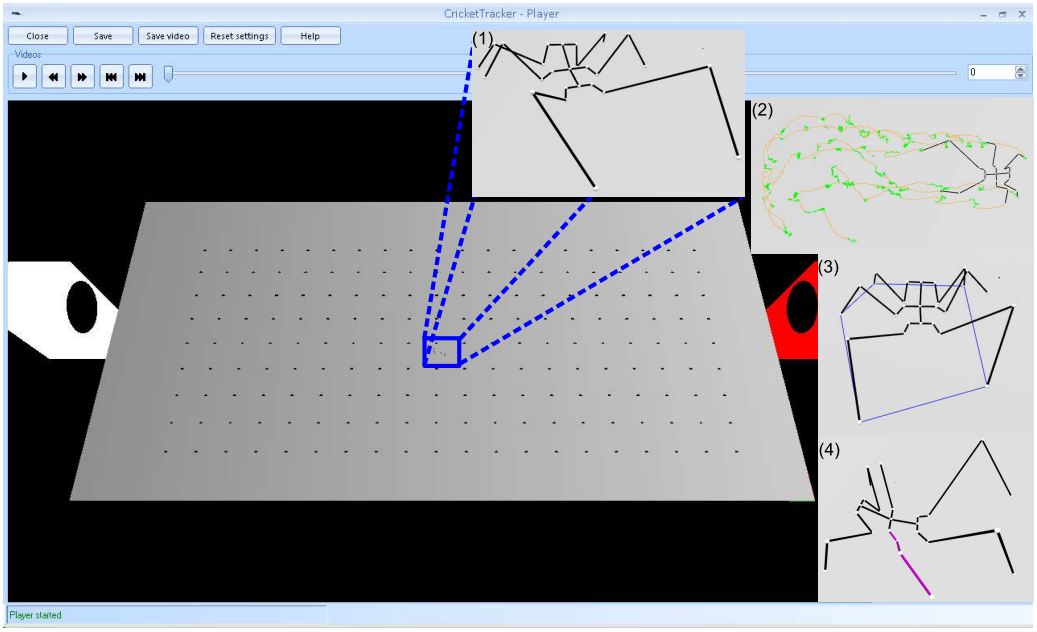


Figure 3.5: A screenshot of the player module of the software. The two boxes represent the speakers. The right speaker is red to indicate that the sound is ON at the specific frame. The player can show various properties of the data such as the path of the insect (2), the stability polygon (3) and the legs that are in swing state (4).

3.4 Results

To illustrate the tracker output, I present results from one recording sequence of the insect. In this scenario the sound is played from the right speaker while the insect starts facing towards the left speaker. When the sequence begins the insect first turns almost on the spot to face the right speaker and then starts walking towards the right speaker until the string is stretched. I processed in total $27 \times 2 \times 6730 + 2 \times 7887 = 379,194$ 2D points for the tracking of the insect and grid points, for these video sequences. I used an HP 6735s laptop (AMD Athlon^{TM}X2 DualCore QL-60 1.9 GHz processor, 4GB RAM). The optimization time for the first frame takes about 20-25 secs and for the subsequent frames 3-6 secs. The following figures show the data produced: the angles of all the body joints (figure 3.6) and for the joints of the front (figure 3.7) , middle (figure 3.8) and hind (figure 3.9) legs; a summary of the stance-swing transitions (figure

3.10); and the reconstructed track and the motion of the feet relative to the body (figure 3.11). From this a number of interesting features can be observed. More detailed analysis of these and other features will be presented in the next chapter.

There is clear movement of the mesothorax, including rhythmic bending of the mesothorax-prothorax joint coupled to the stepping pattern in forward walking (figure 3.6). Both metathorax and mesothorax exhibit some roll into the turn. I should also note that there is clear movement of the abdomen, neck and antennae in all the videos but the monitoring of these movements is beyond the scope of the current experiments.

There are obvious differences between turning and forward walking. During forward walking all body and leg joints follow a regular pattern, while in the case of turning there is much more variability in the values of the angles. However, it is evident that all DoF are used in both forward walking and turning. The data are broadly consistent with previous analyses of a cricket performing forward walking without sound stimulus (Laksanacharoen et al., 2000), except that a clearer contribution of the ThC joint to the hind-leg motion, and of the CTr joint to the front leg motion is observed.

In the approach to sound, there are at most two legs at a time in swing phase and the insect never achieves a tripod gait (figure 3.10). There is no apparent coupling between the chirp pattern and the onset of the stepping cycles (figure 3.10). From the stance patterns, and in figure 3.8, it is obvious that the ipsilateral middle leg is not stepping much during the turn, whereas the contralateral front and middle legs take a higher number of steps, and both hind legs take fewer steps. This is in contrast to experiments on a trackball (Witney and Hedwig, 2011). The ipsilateral hind leg also makes smaller movements during turning. In figure 3.11 it is apparent that the front and middle legs ipsilateral to the sound pull the body towards the speaker direction, while the contralateral front and middle legs push the body. Similar contribution of the middle legs has been observed in cockroaches (Mu and Ritzmann, 2005) and stick insects (Gruhn et al., 2009).

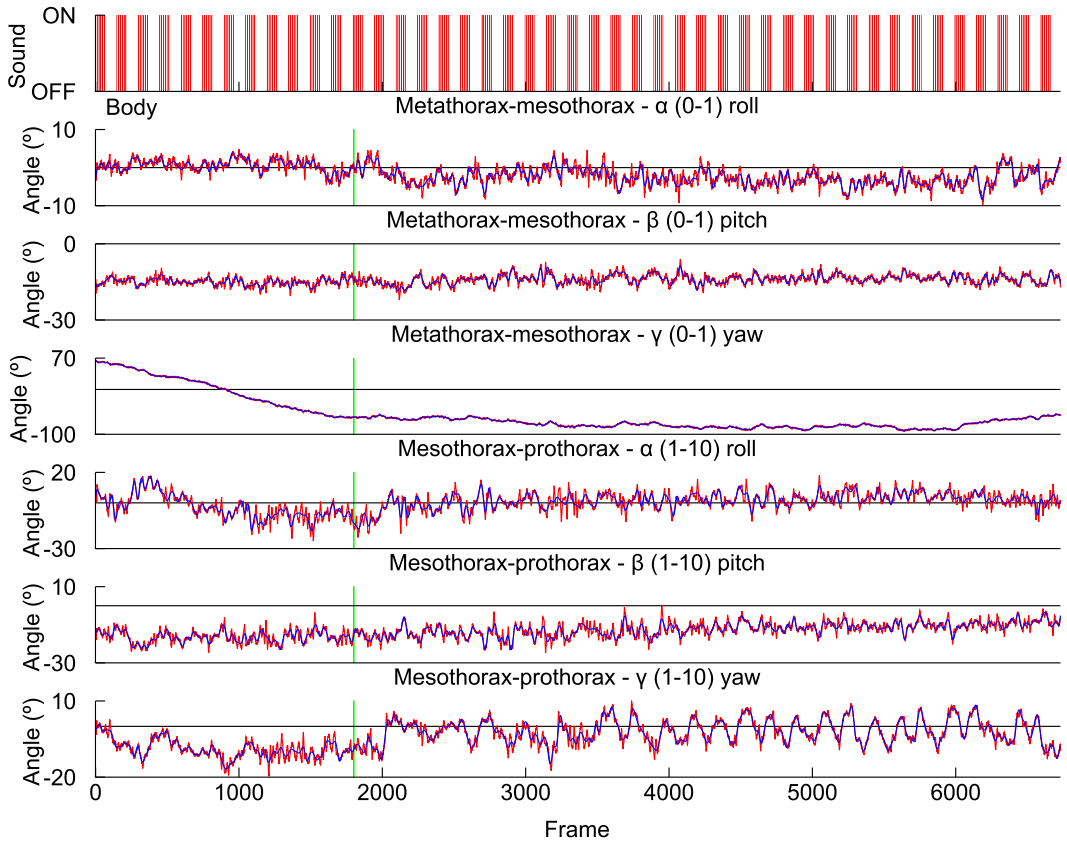


Figure 3.6: Results for the body joint angles: red line is raw data and blue is smoothed data. The green line indicates the end of a right turn by the insect and the beginning of the forward walking towards the sound source. Each frame corresponds to 3.33 ms.

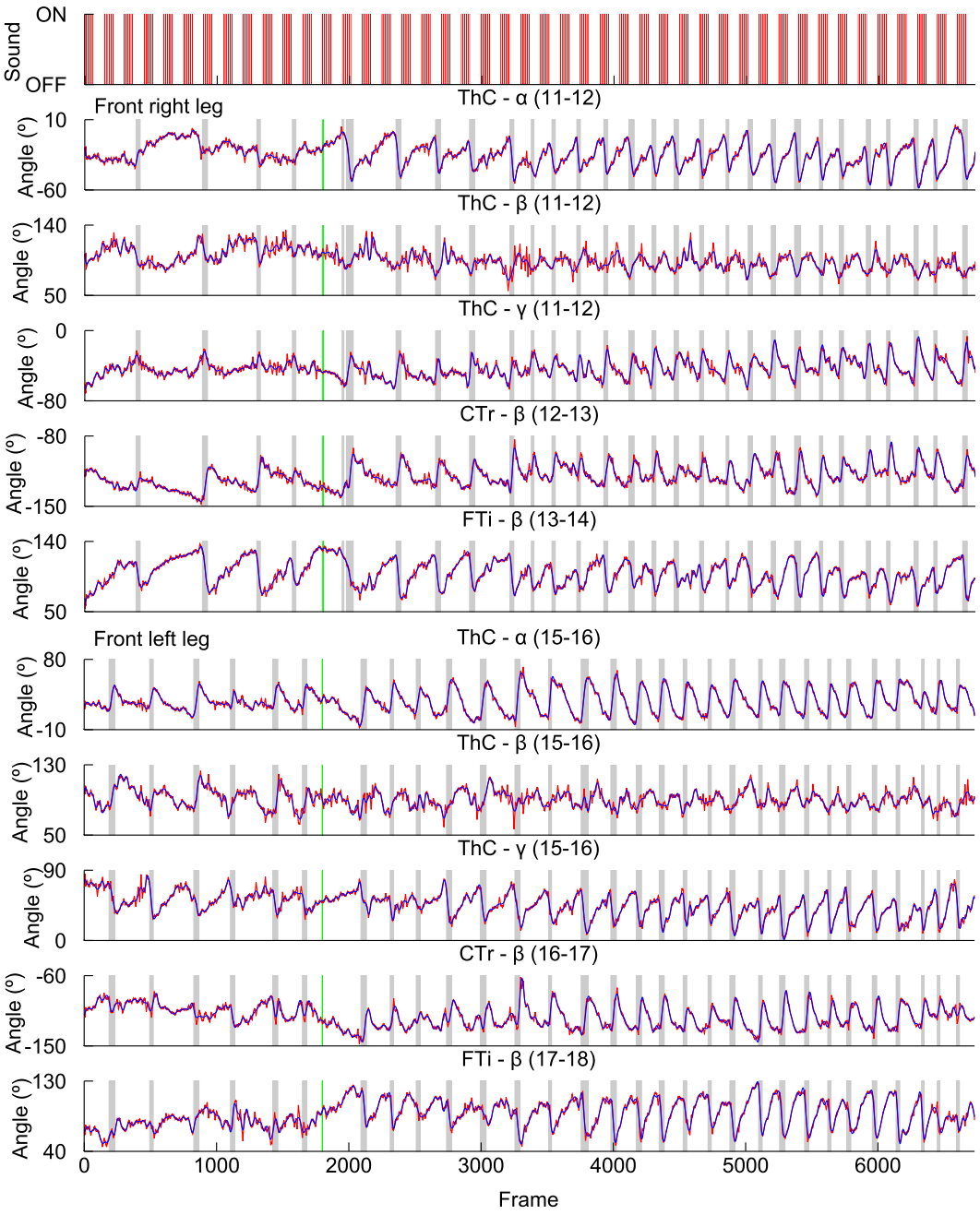


Figure 3.7: Results for the front legs' joint angles: red line is raw data and blue is smoothed data. The green line indicates the end of a right turn by the insect and the beginning of the forward walking towards the sound source. The grey rectangles represent the swing phases for each leg. Each frame corresponds to 3.33 ms.

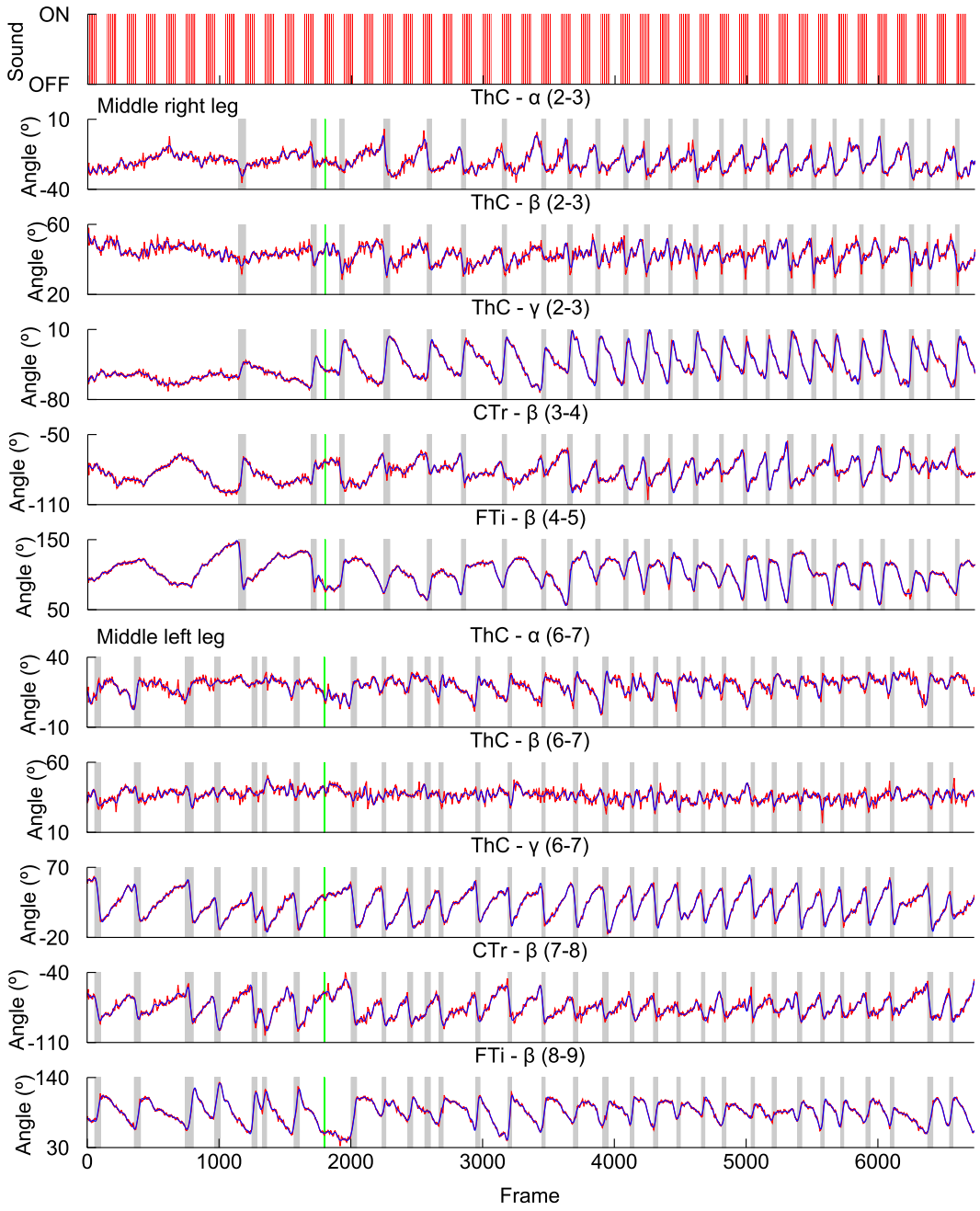


Figure 3.8: Results for the middle legs' joint angles: red line is raw data and blue is smoothed data. The green line indicates the end of a right turn by the insect and the beginning of the forward walking towards the sound source.The grey rectangles represent the swing phases for each leg. Each frame corresponds to 3.33 ms.

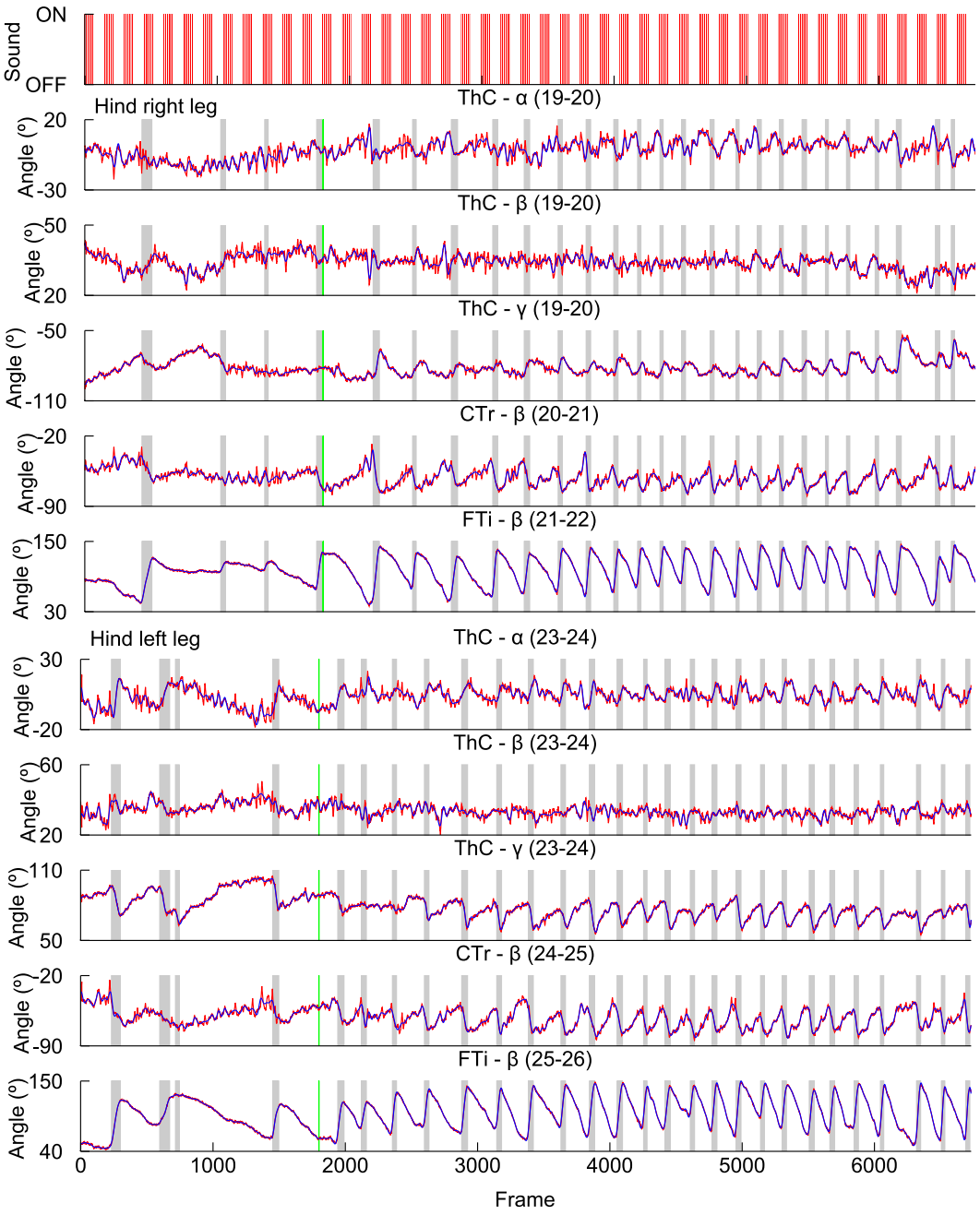
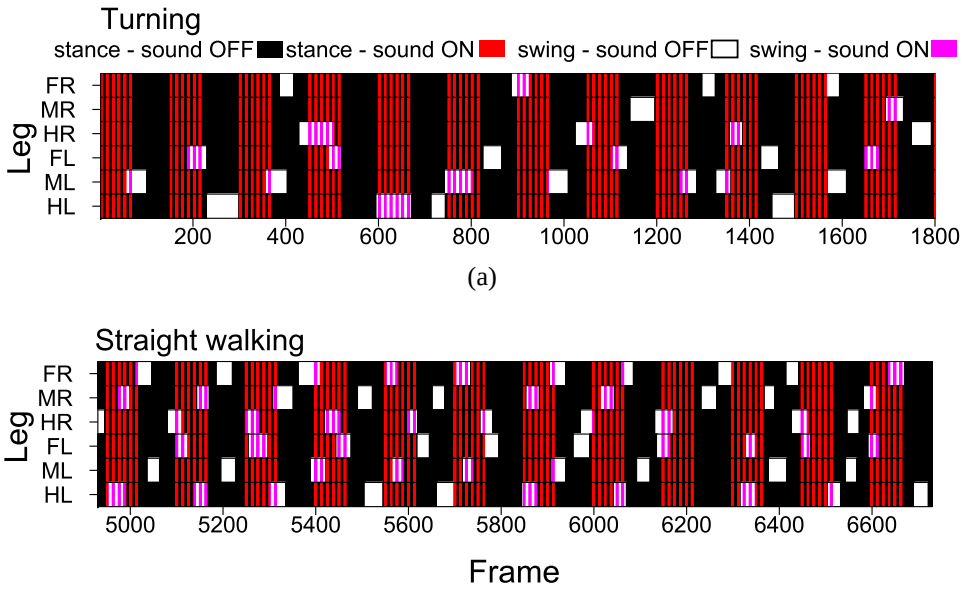


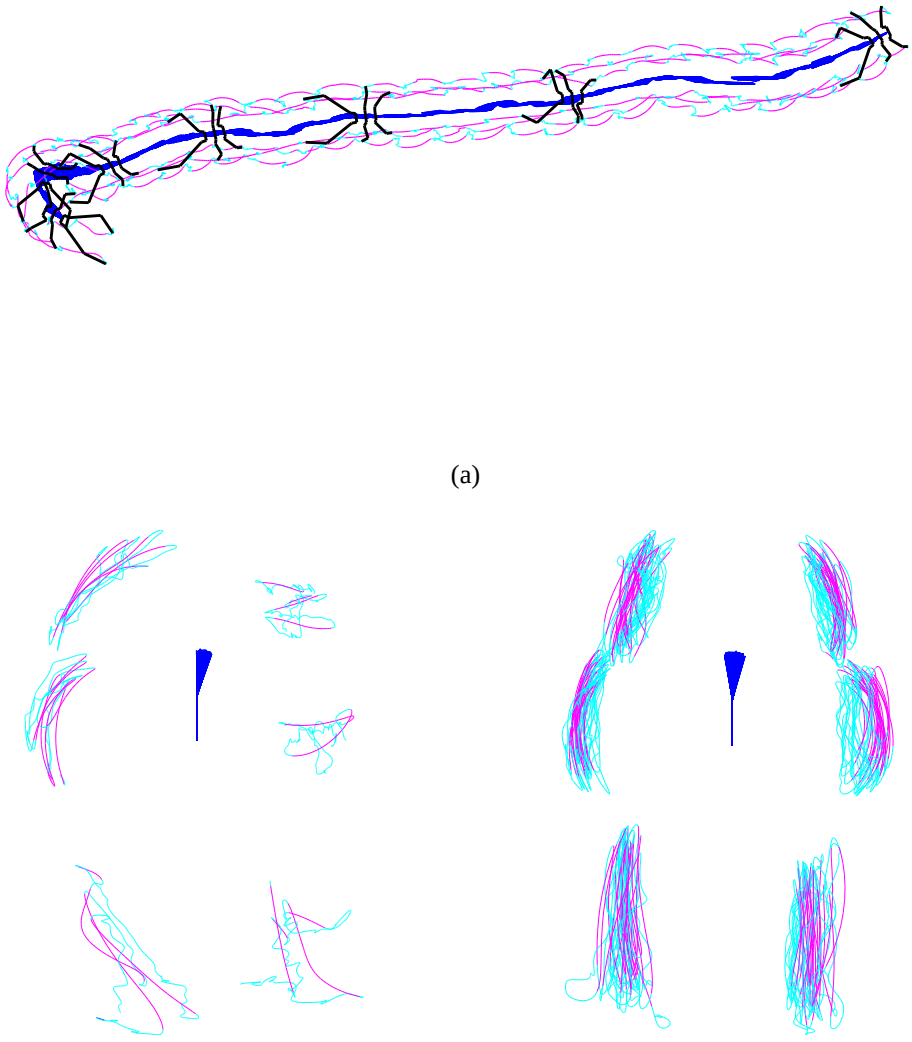
Figure 3.9: Results for the hind legs' joint angles: red line is raw data and blue is smoothed data. The green line indicates the end of a right turn by the insect and the beginning of the forward walking towards the sound source. The grey rectangles represent the swing phases for each leg. Each frame corresponds to 3.33 ms.



(a)

(b)

Figure 3.10: The stance swing transitions for all the legs for (a) right turn and (b) forward walking for the first and last 1800 frames (12 secs) for the same walking sequence as in figures 3.6-3.9. Stance with sound off is marked with black and with sound on with red colour. Swing with sound off is marked with white and swing with sound on is marked with purple colour. From top to bottom, front right (FR), middle right (MR), hind right (HR), front left (FL), middle left (ML) and hind left (HL). Notice in the turn the higher number of swing transitions of the left side legs compared to the right legs and the speed of the legs during swing phase in general. Each frame corresponds to 3.33 ms.



(a)

(b) (c)

Figure 3.11: The transformed smoothed (a) path from the combination of tracking information and the grid points, using the TiTa joints and the thorax joints. The cyan colour indicates the stance phase of the legs, the purple colour the swing phase and the blue colour the thorax position. I can also reconstruct the position of the insect as it would be fixed in one position by simply resetting the translation and rotation of the metathorax. These are the smoothed results taken from the walking sequence shown in (a) and separated into the turning (b) and walking (c) component of the sequence. This allows the comparison of the performance with trackball results such as those by Witney and Hedwig (2011).

Finally, I compare the joint position and angle estimates resulting from the tracker to the same points estimated by manual digitisation. I digitised every tenth frame throughout the sequence, providing a total of 500 estimates of the tracking 'error' for each joint. As shown in figure 3.12(a), the difference was in general less than 0.5mm, with the largest differences occurring for the hind CTr joint still less than 1mm. This compares favourably to the results in Bender et al. (2010) which fall between 0.5mm and 1.5mm. However, note that this could as well be interpreted as the size of 'human error' relative to the automated tracking and model fitting as vice-versa; in particular, fitting the model is essentially a method that corrects for any errors in precise localisation of the marker. I then used the law of cosines to estimate the maximum difference in estimates of angles that could be produced by the observed difference in the position estimates (figure 3.12(b)).

$$\arccos \frac{2 \times segmentLength^2 - jointDifference}{2 \times segmentLength^2} \tag{3.10}$$

Note that for each joint this is done for one degree of freedom. Therefore for 3 DoF joints (ThC) I am estimating based on a 'worst case' scenario in which the error is assumed to be entirely due to one of these DoF while the other two have zero error. Not surprisingly, given that the coxa segments are quite small (for example hind coxa is 1.6 mm), this methods results in a relatively large maximum error estimate for the ThC joint angles.

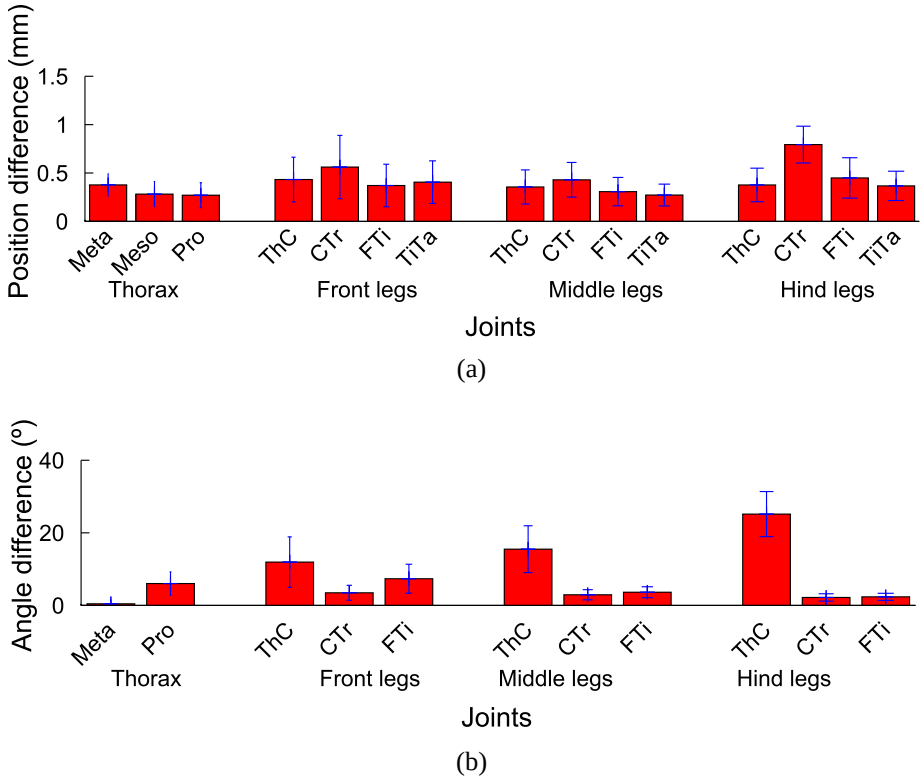


Figure 3.12: (a) Deviation in tracking acuity (in mm) by the tracking algorithm compared to manual digitization for 500 frames. The difference is generally less than 0.5 mm. (b) Estimated maximum error in joint angles (in degrees) that could result from the observed deviation in tracking acuity.

Chapter 4

Analysis

4.1 Introduction

In the previous chapter I described a method to track the joints of a female cricket while it performed phonotaxis. In this chapter I present an analysis based on the results from all the videos I recorded when the crickets responded to the sound signal. All specimens were given up to 5 minutes to respond. These results are based on 16 different crickets. There are 2 experiments per cricket and therefore 32 experiments in total. Sound was presented 19 times from the right speaker and 13 from the left speaker. There are 17 right turns and 15 left turns. There are four combinations of speaker - turn direction (11 times right speaker - right turn, 8 times right speaker - left turn, 6 times left speaker - right turn and 7 times left speaker - left turn). The first 8 crickets were tracked for both turning and forward walking, while the last 8 crickets were tracked only for the initial turning, to gather more information and samples regarding the turning behaviour. In total, 308,398 grid points and 4,902,768 tracker points were obtained, giving a total of 5,211,166 2D points, resulting in 2,605,583 3D points, most of which were tracked by the tracking software.

Table 4.1 presents a summary of the overall video processing. I define turn latency as the period from the first sound pulse played by the speaker until the first antennal movement. Only one cricket responded to the first chirp. Average turn latency was 52.54$\pm$55.55 sec (mean$\pm$SD) with maximum latency 208.13 sec, minimum latency 0.27 sec, median latency 34.84 sec and kurtosis 3.14 (for distributions see figure 4.1). Average turn duration was 3590.63$\pm$1636.09 ms with maximum duration 8570 ms, minimum duration 1636.09 ms, median duration 3815 ms and kurtosis 3.85 (for distributions see figure 4.1). These values take into account periods when some of

the crickets had stopped during the turn. Most crickets did not stop after the turn (N=27) but about half of them stopped at least one time during turning or forward walking (N=14). This is in contrast with earlier studies where there was no discontinuity in the movement between the turn and subsequent forward walking (*Scapsipedus marginatus*; Murphey and Zaretsky, 1972). I defined a stop as a period of at least 90 frames (≈300 ms), a value within the stepping cycle reported in earlier studies (Laurent and Richard, 1986b; Witney and Hedwig, 2011), where all the legs were touching the ground and the rest of the body was not moving. These results include the crickets that were tracked only during turning but the videos also include their forward walking behaviour and therefore I was able to determine the number of times they had stopped.

Although not explicitly tracked, it was observed in the videos that the insects' antennae are the first moving part and scan the area in front of the head. The time taken from the first move of the antennae until the cricket lifted its first leg in order to turn was between 10 and 1806 ms with a mean value 443.54±416.9 ms, median value 346.67 ms and kurtosis 5.8 (for distributions see figure 4.1). Both antennae turn towards the direction of turning when the cricket initiates its turn. Also, head orientation is shifted towards the turning direction. This lead response of the antennae and the head has been observed before in stick insects (Dürr and Ebeling, 2005).

In the following sections, I address specific questions that were posed in chapter 2. Note that a direct comparison with results from other studies on crickets or other insects is not possible, since the methodologies followed either use more constraints on the insect motion and therefore movements are not exactly similar to freely walking conditions, or if the insect is walking freely the study does not provide the amount of information gained with the method followed in this thesis. First I analyse the results of the individual leg and body angles (section 4.2). Then I present the leg coordination results (section 4.3). Furthermore, I analyse the angles of the thorax and the ears in the front legs with respect to the centre of the speakers (section 4.4). Finally, I present an estimation of the ears input while the cricket performs its phonotactic response (section 4.5).

C	E	S	TD	TL	TF	FT	TT	TS	SN	AM
01	01	R	R	13890	7944	6731	1801	0	0	106
01	02	L	R	8003	6593	5251	431	0	0	103
02	01	L	L	28927	6593	5641	1474	281	1	72
02	02	R	L	31059	10040	9311	1051	0	2	338
03	01	R	R	12898	5395	4901	621	0	1	53
03	02	L	R	6681	4796	4311	583	0	1	10
04	01	R	R	2928	3147	2561	480	0	0	3
04	02	L	L	2447	4945	4301	852	941	1	105
05	01	R	R	21692	5994	4091	1471	0	0	161
05	02	L	L	19294	8092	7171	2571	0	1	542
06	01	R	R	4116	5844	4201	1351	0	0	159
06	02	L	L	4553	4496	2861	583	0	1	96
07	01	R	L	1561	3746	3161	561	0	0	60
07	02	L	R	384	3896	3091	1281	0	1	123
08	01	R	R	311	3896	2751	1186	0	0	458
08	02	L	R	489	3297	2271	582	0	1	17
09	01	L	R	22262	2247	971	884	0	0	33
09	02	R	L	39280	3296	1701	1680	0	0	69
10	01	L	L	13012	3597	1841	1841	0	0	192
10	02	R	R	26658	2397	911	911	0	0	61
11	01	R	R	82	1799	861	861	0	0	106
11	02	R	L	179	2247	1261	1232	0	0	234
12	01	R	L	4649	9140	541	436	0	2	49
12	02	R	L	31329	5850	1281	1148	881	2	84
13	01	L	L	41469	2098	1191	1191	0	0	216
13	02	R	L	16684	1348	671	620	0	0	41
14	01	R	R	479	2847	1401	1374	0	0	12
14	02	R	R	39628	4495	1391	1322	0	0	157
15	01	R	L	44724	10039	1231	1231	0	2	231
15	02	L	L	62439	9740	1211	1211	1235	2	205
16	01	L	R	574	1648	581	508	0	0	11
16	02	R	R	1718	2697	1141	1141	271	1	151

Table 4.1: Time properties for all the experiments. Cricket number (C), experiment number (E), speaker(S), left (L), right (R), turn direction(TD), turn latency(TL), total frames (TF), tracked frames (FT), turn time frames (TT), stop duration after turn in frames (TS), number of stops (SN) and antennae and head movement frames before first leg swing (AM). Each frame corresponds to 3.33 ms.

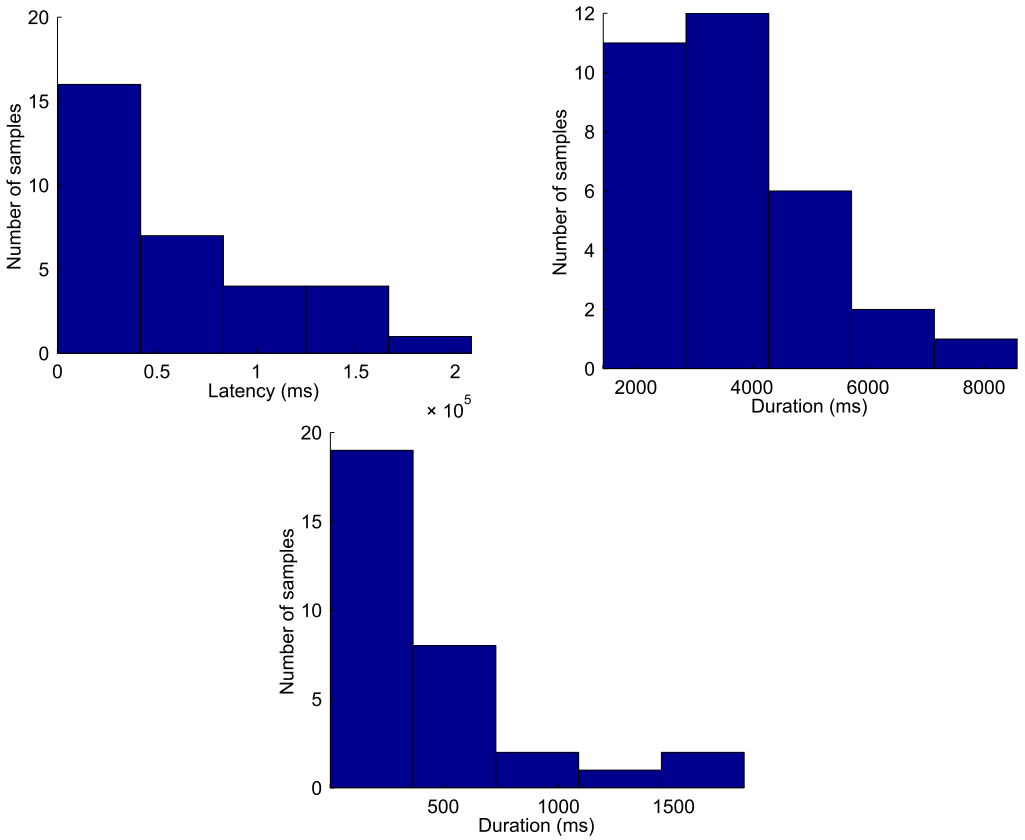


Figure 4.1: Distributions of time properties for all the experiments. Turn latency (top left), turn duration (top right) and antennae movement (bottom).

4.2 Single Leg and Body Angles

In this section I address the following questions:

- What is the motion of each thoracic segment and body part during forward walking and turning?
- What is the motion of each individual leg joint during forward walking and turning?
- What are the similarities and differences with other insects?

I distinguish between the initial left and right turn when the crickets turn to orient themselves towards the sound source and the rest of the walking behaviour which is termed as forward walking. Note that the walking patterns produced are never perfectly straight and each side of the insect does not produce exactly the same body and leg joint

patterns. I define the beginning of turning as the time when the insect begins moving its antennae and head. In order to determine the end of turning, I inspected the videos and the 3D reconstruction of the insect in the Player module, to find when the insect began walking approximately forward after the initial turn. All the legs had completed their step cycle before the defined end of the turn. In most turns the crickets either turn on the spot or produce a U-shaped turn pattern similar to previous results on honeybees' turning behaviour (Zolotov et al., 1975). However, in contrast to the aforementioned study and results from tethered stick insects (Gruhn et al., 2009) and freely walking flies (Strauss and Heisenberg, 1990), it was observed that the ipsilateral middle leg halted during turning rather than the ipsilateral hind leg.

I first gathered the periods where each leg was in swing mode. Then, based on the coordinates of the TiTa joints at the beginning and at the end of swing I calculated the average distance that each leg had travelled. The same procedure was also performed for the trackball coordinates (*i.e.* distances relative to the cricket's own body). Furthermore, I calculated the number of swing transitions that each leg had made.

It is clear that during right turns the left legs from all the thoracic segments cover longer distance than those on the right side (table 4.2) and correspondingly the opposite case happens during left turns. This is in contrast with results from stick insects where the front contralateral to the turn leg had the same stride length as forward walking (Gruhn et al., 2009). Change in the step length on one side relative to the other has been observed before in experiments in stick insects (Graham, 1972) and cockroaches (Franklin et al., 1981) and on a trackball in crickets (Witney and Hedwig, 2011). During forward walking both sides cover the same distances. The front and the middle legs cover similar distances, while the hind legs cover slightly longer distances. This is easily explained by the length of the leg segments. However, the trajectory of the front and middle legs is more like an arc and the hind legs' is closer to a straight line (figure 4.2).

If the same properties are calculated for the converted trackball coordinates, they produce similar results (table 4.3). The only difference is that the legs cover smaller distances. This is expected because if the insect is fixed on a trackball, its body is not moving forward as the legs move.

The number of swings and the timing of the leg movements also reveals the contribution of each leg to turning (table 4.4). The most clear difference with respect to turning regards the middle legs. The middle leg ipsilateral to the turn is lifted off the ground only a quarter to a half as many times as the contralateral middle leg, as the

L	RT MV	RT SD	LT MV	LT SD	FW MV	FW SD
FR	4.74	±1.46	6.83	±2.05	8.47	±2.68
FL	7.21	±2.47	4.76	±1.82	8.50	±2.98
MR	5.26	±1.86	6.69	±2.22	8.38	±3.11
ML	7.49	±2.13	4.65	±1.98	8.26	±3.07
HR	5.13	±1.99	8.46	±2.00	9.38	±2.88
HL	9.78	±2.57	5.37	±2.22	9.64	±2.79

Table 4.2: Mean values (MV) and standard deviations (SD) of swing distances for the front right (FR), front left (FL), middle right (MR), middle left (ML), hind right (HR) and hind left (HL) legs (L) in millimetres, during right turn (RT), left turn (LT) and forward walking (FW). Note some variation is due to different size animals.

L	RT MV	RT SD	LT MV	LT SD	FW MV	FW SD
FR	3.74	±1.25	5.63	±1.62	5.81	±1.61
FL	6.01	±2.11	3.78	±1.51	5.90	±1.87
MR	4.45	±1.51	5.30	±1.80	5.73	±2.02
ML	5.99	±1.71	3.96	±1.70	5.62	±2.04
HR	4.32	±1.69	7.10	±1.83	6.87	±2.11
HL	8.23	±2.05	4.33	±1.80	7.22	±1.92

Table 4.3: Mean values (MV) and standard deviations (SD) of trackball swing distances for the front right (FR), front left (FL), middle right (MR), middle left (ML), hind right (HR) and hind left (HL) legs (L) in millimetres, during right turn (RT), left turn (LT) and forward walking (S). Note some variation is due to different size animals.

insect turns to orient itself towards the speaker. This is in contrast with experiments on a trackball (Witney and Hedwig, 2011) where no change in stepping frequency was found. The front and the hind legs produce almost the same number of swings during turning and forward walking, although with slightly less number of swings on the ipsilateral to the turn side. Also the hind legs produce fewer swings compared to front legs during turning.

In terms of timing, the front and the middle legs take a similar amount of time for their swing during turning and the hind legs take more time. During forward walking the front and the hind legs take the same amount of time to perform their swing while the middle legs take less time. The ratio of protraction/retraction is significant lower for the ipsilateral to the turn middle leg as expected (table 4.5). During forward walking

L	RT N	RT MV	RT SD	LT N	LT MV	LT SD	FW N	FW MV	FW SD
FR	80	80.38	±25.91	79	84.68	±28.20	433	82.22	±19.65
FL	87	77.97	±26.09	73	92.92	±33.60	450	82.26	±19.52
MR	23	78.41	±28.94	80	78.67	±25.65	426	67.21	±19.70
ML	76	78.33	±28.71	39	74.19	±21.04	432	65.88	±18.06
HR	54	99.63	±40.74	64	114.01	±35.94	432	81.64	±19.11
HL	63	114.07	±40.41	55	114.42	±50.17	427	81.52	±20.66

Table 4.4: Number of swings (N), mean values (MV) and standard deviations (SD) of swing duration for the front right (FR), front left (FL), middle right (MR), middle left (ML), hind right (HR) and hind left (HL) legs in milliseconds, during right turn (RT), left turn (LT) and forward walking (FW).

the ratio is similar for the front and hind legs. This in contrast with previous results in crickets (*Acheta domesticus*; Harris and Ghiradella, 1980) and cockroaches (Delcomyn and Usherwood, 1973) where the hind legs spend more time during forward walking in swing than the front and middle legs. This might be explained by the fact that even if the hind legs are longer, the front legs have larger range of movements. Also since the percentage of each leg on the ground is very different for the middle legs this is in contrast with results in cockroaches (Franklin et al., 1981) where all six legs had similar protraction/retraction rates during turning.

L	RT MV	RT STD	LT MN	LT STD	FW MN	FW STD
FR	0.22	±0.17	0.19	±0.10	0.32	±0.17
FL	0.25	±0.33	0.24	±0.38	0.33	±0.13
MR	0.07	±0.04	0.25	±0.49	0.25	±0.16
ML	0.26	±0.36	0.09	±0.06	0.25	±0.11
HR	0.20	±0.29	0.26	±0.25	0.31	±0.10
HL	0.23	±0.15	0.18	±0.13	0.30	±0.11

Table 4.5: Mean values (MV) and standard deviations (SD) of ratio of protraction / retraction during right (RT) and left (LT) turns and forward walking (FW).

In order to calculate the change in angle of each joint during each stride I first grouped all the samples of angles that are from the beginning of stance to the end of swing for the left and right turns and forward walking. I did not take into account the periods when the insects were stopped. Then, I used cubic spline interpolation

provided by the MATLAB's spline function to resample the angle values into 100 values for each sample. Then I calculated the mean and standard deviation of these samples. There are 180 figures in total (5 joints per leg $\times$ 6 legs $\times$ 3 types of walking + 5 body angles $\times$ 6 legs $\times$ 3 types of walking), most of which are provided in pages 70–77. I present three columns with figures for the forward walking in the left, right turn in the middle and left turn in the right. Because each insect only made a few steps during its initial turn, there are obviously fewer samples for the turns than for the forward walking. This is especially salient for the inside middle legs during the corresponding turn, since the leg is lifted off the ground very few times.

Many of the joint movements of the cricket are different between forward walking and turning. During forward walking the legs of each thoracic pair make similar movements, while during turning there are obvious differences between all three pairs of legs. This in contrast with experiments on a trackball (Witney and Hedwig, 2011) and an arena (*Scapsipedus marginatus*; Murphey and Zaretsky, 1972) in crickets and stick insects (Dürr and Ebeling, 2005) where only the front and middle legs presented changes. This can possibly be explained by the fact that the hind legs are the ones affected most by the movement of the trackball. Also, the low temporal resolution of the video recordings in earlier studies in an arena may have limited the accuracy of the leg trajectory tracking.

The front leg ipsilateral to the turn direction increases its lateral movement while it decreases its forward movement (figure 4.2). The front leg contralateral to the turn direction increases its forward and lateral movement. The middle leg ipsilateral to the turn is rarely lifted off the ground during turning and presents the smallest movement of all the legs; decreasing its forward movement and increasing its lateral movement. In contrast, the middle leg contralateral to the turn increases its forward and lateral movement. The hind leg ipsilateral to the turn decreases its forward movement and increases its lateral movement. The hind leg contralateral to the turn increases its forward and lateral movement. The prothorax moves towards the direction of the turn. It is worth noting that during turns the ipsilateral to the turn middle leg's TiTa joint is the centre of a circle formed by the stance points. This fact suggests that a two-wheeled robot that limits the movement or even stops one of its wheels is actually a reasonable approximation to the crickets turning behaviour.

The results of the individual joints show obvious differences during forward walking, left turn and right turn. I will refer to the differences in the pattern in the right side for every thoracic segment. This means that for the right turn this will be the inside leg

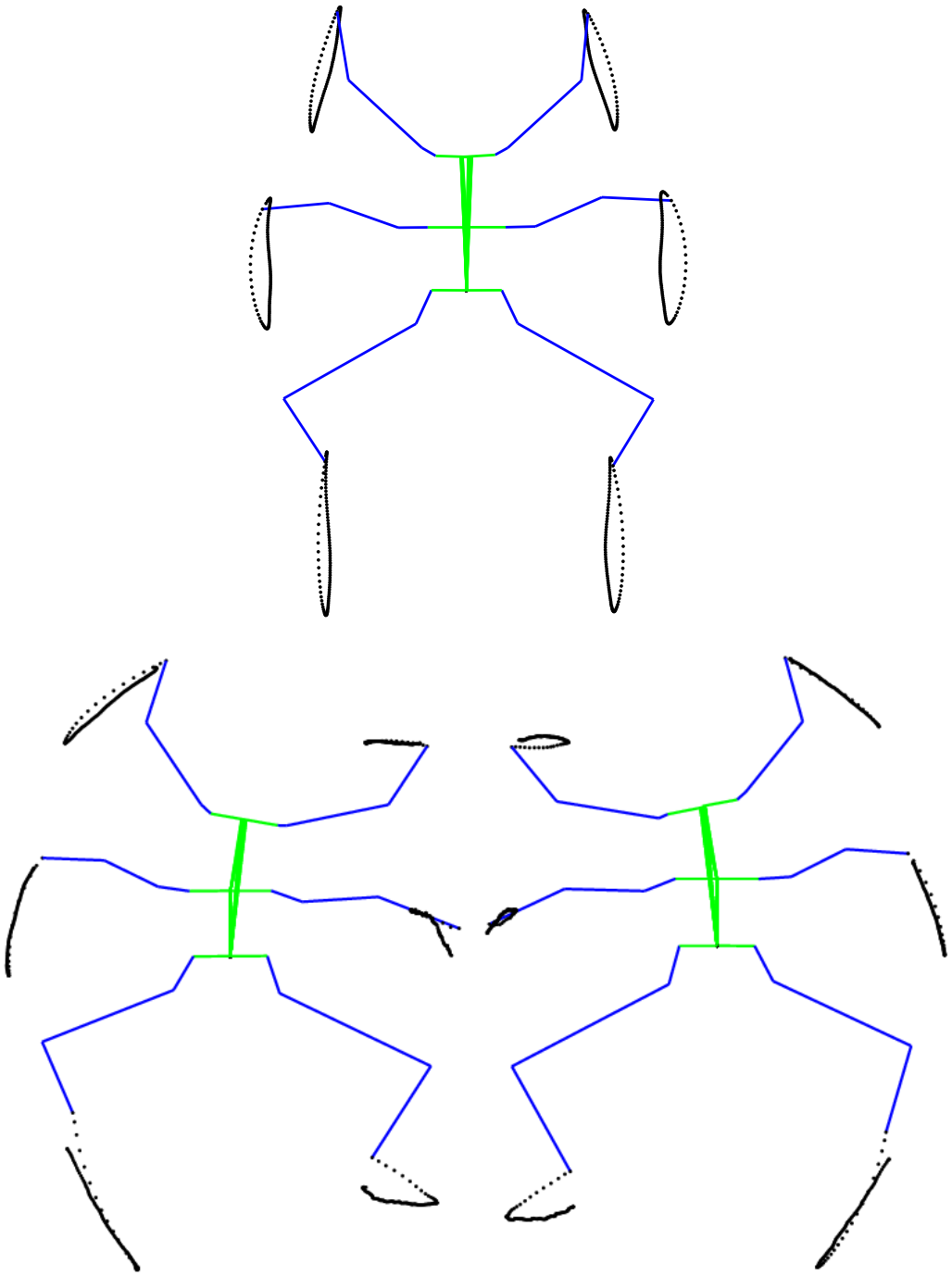


Figure 4.2: Top view of leg patterns during forward walking (top), right turn (bottom left) and left turn (bottom right). Thorax is depicted with green colour, legs with blue and trajectories with black. Note that the stance segments during turns appear to fall on a circle with its centre to the ipsilateral to the turn middle leg's TiTa joint.

and for the left turn the outside leg. The differences in the left side are similar, given that some of the joints are expected to have the exact opposite pattern. For instance the

ThC_α have opposite patterns in all the leg pairs. The results for the middle legs when the leg is ipsilateral to the turn side are the noisiest ones since there are less samples for the middle legs.

I will now briefly mention the effect of each joint DoF to the leg and body movement, before presenting the results. ThC_α rotates the coxa around its long axis. ThC_β moves the coxa up or down. ThC_γ moves the coxa forwards or backwards. CTr_β moves the femur up or down. FTi_β moves the tibia in or out. Metathorax - $mesothorax_\alpha$ rotates the metathorax - mesothorax segment around its long axis. Metathorax - $mesothorax_\beta$ moves the metathorax - mesothorax segment up or down. Mesothorax - $prothorax_\alpha$ rotates the mesothorax - prothorax segment around its long axis. Mesothorax - $prothorax_\beta$ moves the mesothorax - prothorax segment up or down. Finally, the mesothorax - $prothorax_\gamma$ moves the mesothorax - prothorax segment right or left. See the first column of the figures in pages 70–77 for visualization.

The front right leg (figure 4.3), during forward walking stance phase increases the ThC_α, ThC_β and FTi_β angles and decreases the ThC_γ and CTr_β angles. Then during swing it decreases the ThC_α, ThC_β and FTi_β angles and increases the ThC_γ and CTr_β angles. During right turn the ThC_α angle remains the same throughout the step. The ThC_β increases during stance and decreases during swing as before. The ThC_γ remains the same during stance until the last part when it increases and decreases during swing. The CTr_β and FTi_β have similar pattern with forward walking. During left turn the ThC_α and ThC_γ have similar pattern with forward walking. The ThC_β is decreased during stance and increased during swing. The CTr_β remains the same during stance and first decreases and then increases during swing. The FTi_β remains constant throughout the step. This observation for the front leg contralateral to the turn has been made before, although in less detail (Witney and Hedwig, 2011).

The middle right leg (figure 4.5), forward walking stance phase increases ThC_α, ThC_β and CTr_β angles while the ThC_γ angle decreases and the FTi_β angle initialy remains stable and then decreases. During swing the ThC_α, ThC_β and CTr_β angles decrease while the ThC_γ and FTi_β angles increase. During right turn the ThC_α and ThC_β remain constant, while the ThC_γ increases during stance and decreases during swing. The obvious differences with forward walking is that the CTr_β decreases during stance and increases during swing while the FTi_β follows the opposite pattern. This has been observed before in cockroach escape response (Nye and Ritzmann, 1992). During left turn all the joints have similar values with the forward walking. The FTi_β has the opposite pattern than right turn.

The hind right leg (figure 4.7), forward walking stance phase increases ThC_{α} and CTr_{β} and decreases ThC_{γ} and FTi_{β}. ThC_{β} remains constant throughout the step cycle. During swing ThC_{α} and CTr_{β} decrease and ThC_{γ} and FTi_{β} increase. During right turn ThC_{α} remains constant while ThC_{γ} increases during stance and decreases during swing. ThC_{β} decreases during stance and increases during swing. CTr_{β} and FTi_{β} angles have similar patterns with forward walking, but smaller range of values. During left turn ThC_{α} and ThC_{γ} have similar values to forward walking. ThC_{β} increases during stance and decreases during swing. CTr_{β} and FTi_{β} values are similar to the right turn values.

In figures 4.9 - 4.10 I present the effect at the body angles relative to the step sequence of the front legs. The effect relative to middle and hind legs is similar. Metathorax - mesothorax$_{\alpha}$ remains the same for forward walking and turning. Metathorax - mesothorax$_{\beta}$ and Mesothorax - prothorax$_{\beta}$ slightly decrease during turning. Mesothorax - prothorax$_{\alpha}$ and Mesothorax - prothorax$_{\gamma}$ have similar patterns during forward walking and turning but with different values, reflecting the bending of the body in the direction of the turn. Therefore the bending of the prothorax contributes to the positioning of the front legs as has been observed before on a trackball (Witney and Hedwig, 2011).

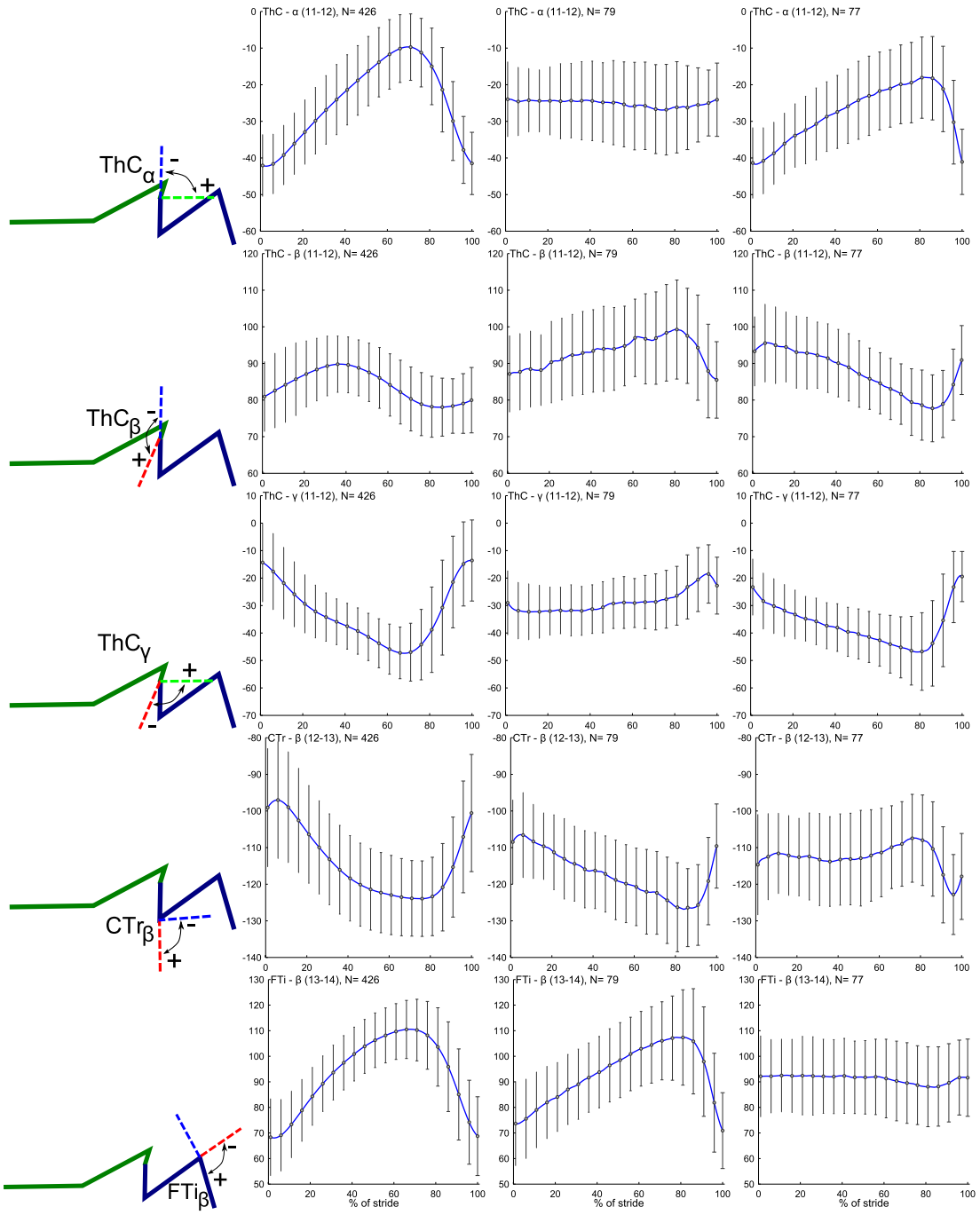


Figure 4.3: Mean, standard deviation of angles values and number of samples (N) for the front right leg during forward walking (left), right (middle) and left (right) turn. 0% represents the start of stance and 100% the end of swing.

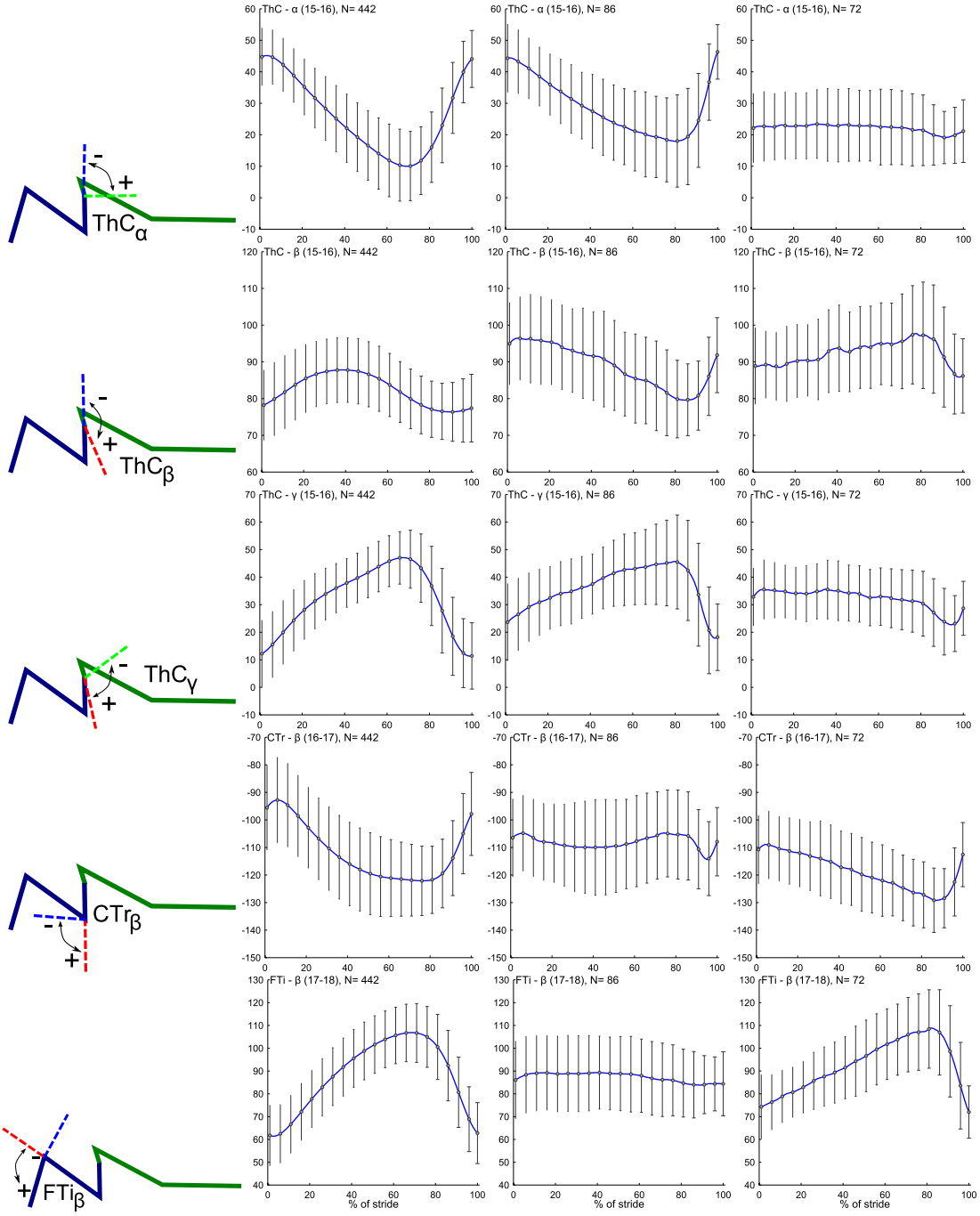


Figure 4.4: Mean, standard deviation of angles values and number of samples (N) for the front left leg during forward walking (left), right (middle) and left (right) turn. 0% represents the start of stance and 100% the end of swing.

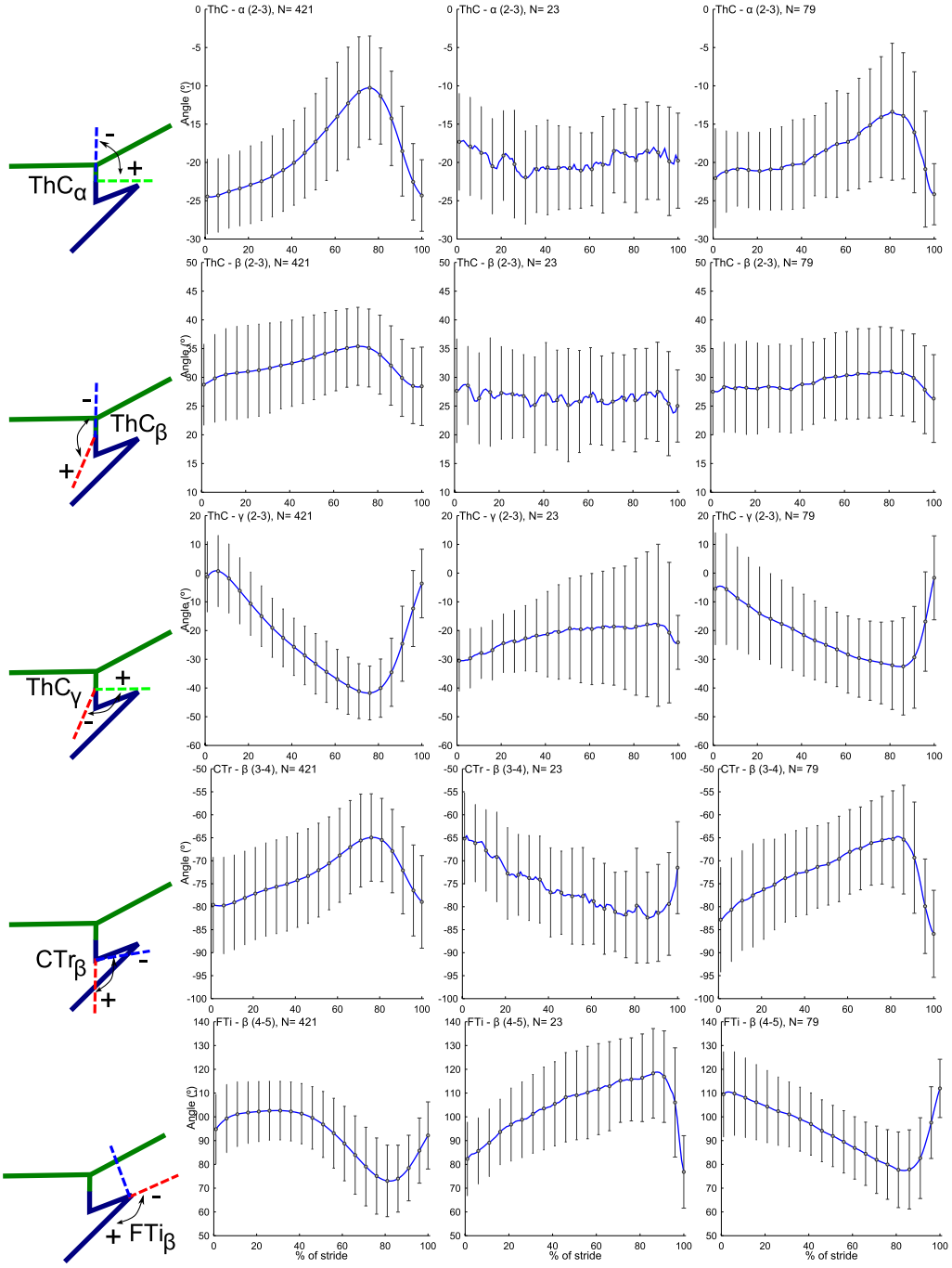


Figure 4.5: Mean, standard deviation of angles values and number of samples (N) for the middle right leg during forward walking (left), right (middle) and left (right) turn. 0% represents the start of stance and 100% the end of swing.

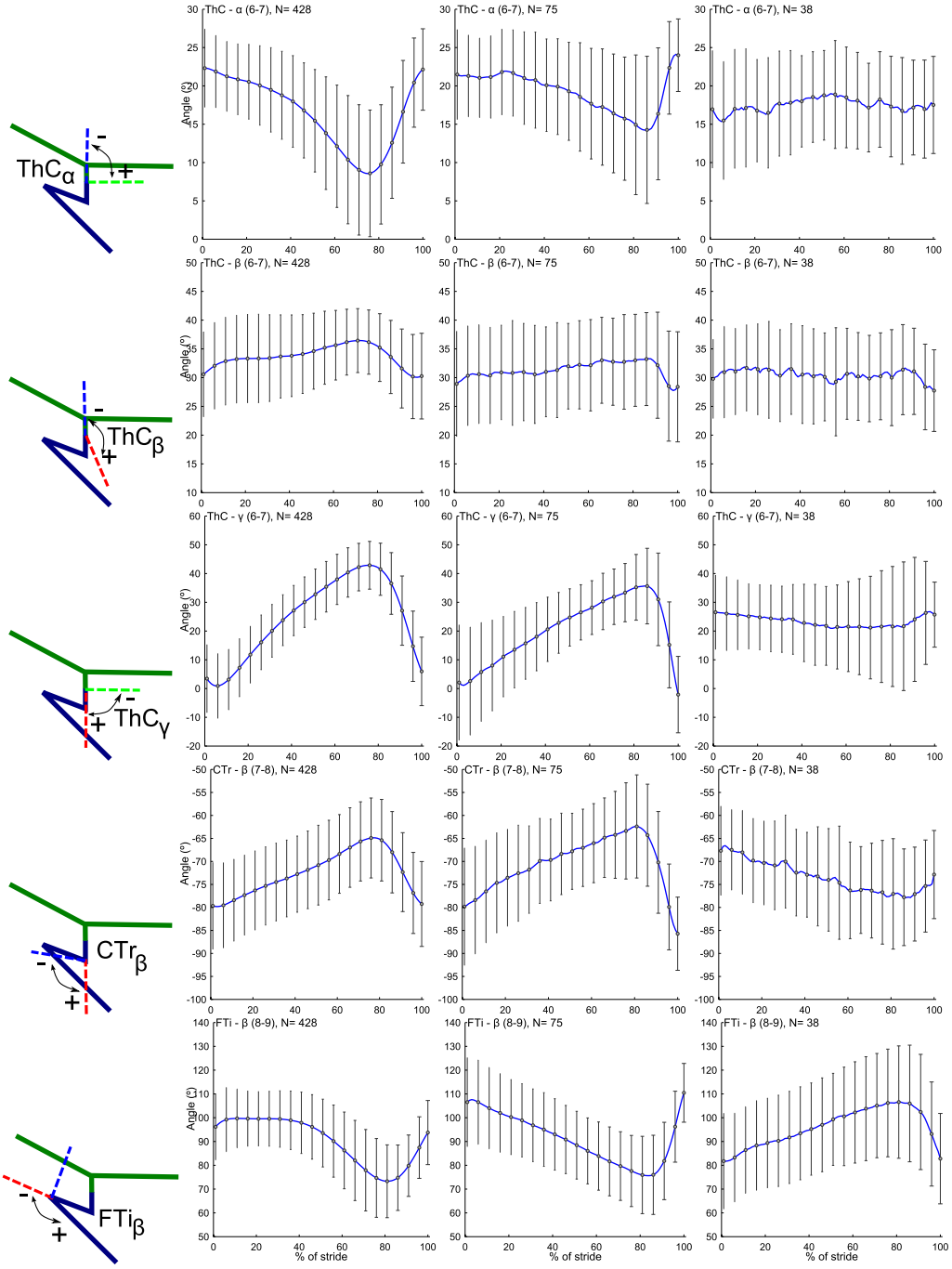


Figure 4.6: Mean, standard deviation of angles values and number of samples (N) for the middle left leg during forward walking (left), right (middle) and left (right) turn. 0% represents the start of stance and 100% the end of swing.

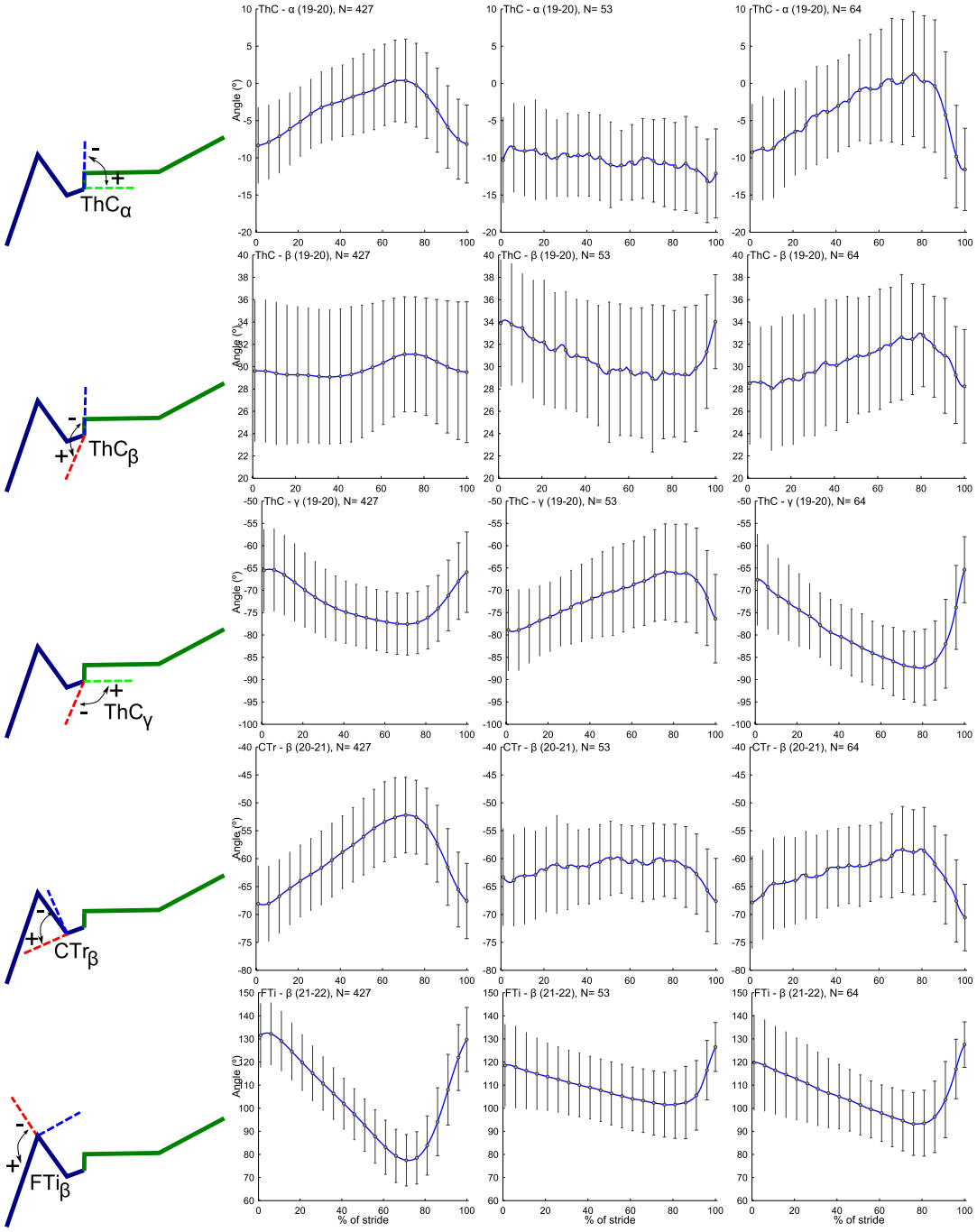


Figure 4.7: Mean, standard deviation of angles values and number of samples (N) for the hind right leg during forward walking (left), right (middle) and left (right) turn. 0% represents the start of stance and 100% the end of swing.

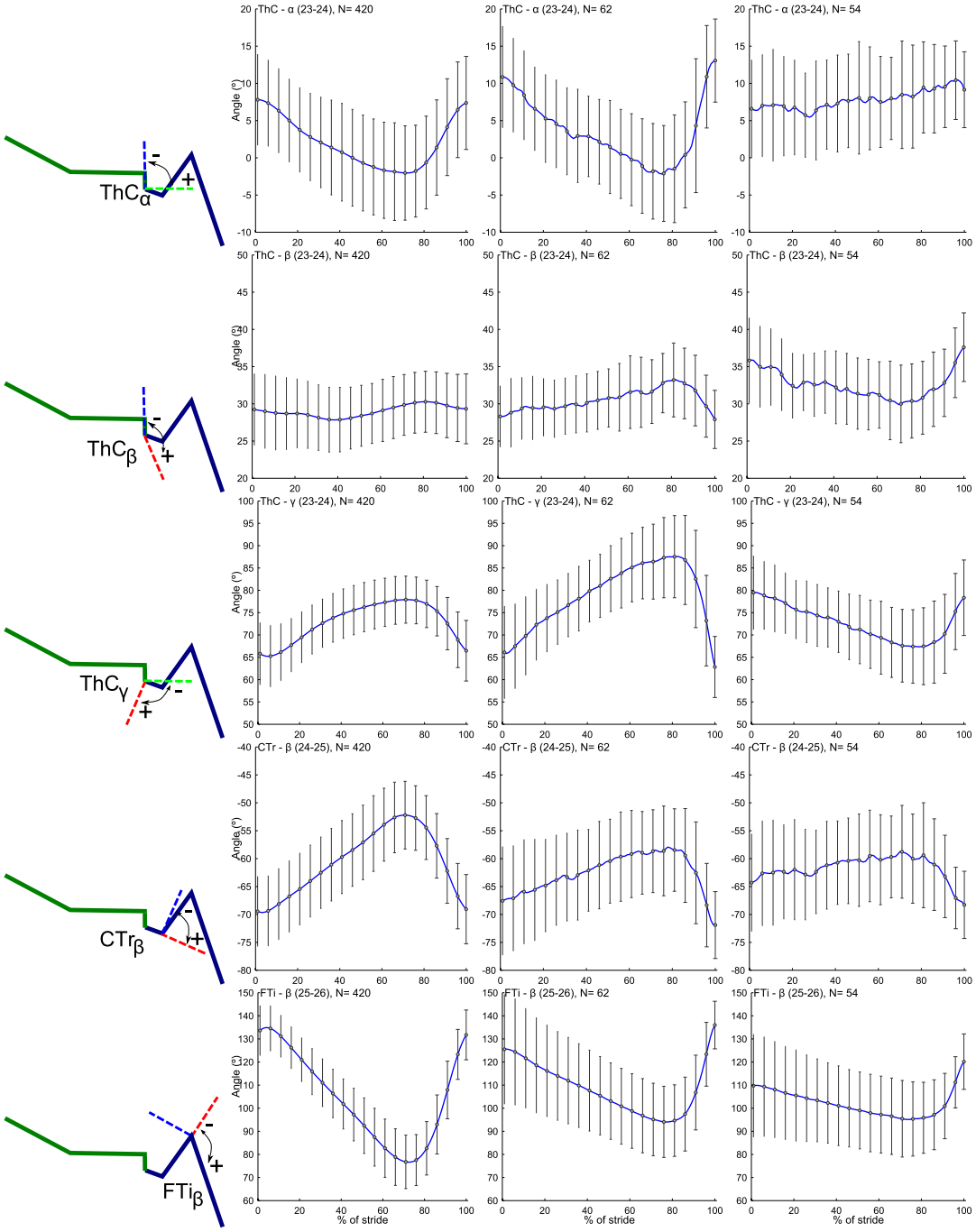


Figure 4.8: Mean, standard deviation of angles values and number of samples (N) for the hind left leg during forward walking (left), right (middle) and left (right) turn. 0% represents the start of stance and 100% the end of swing.

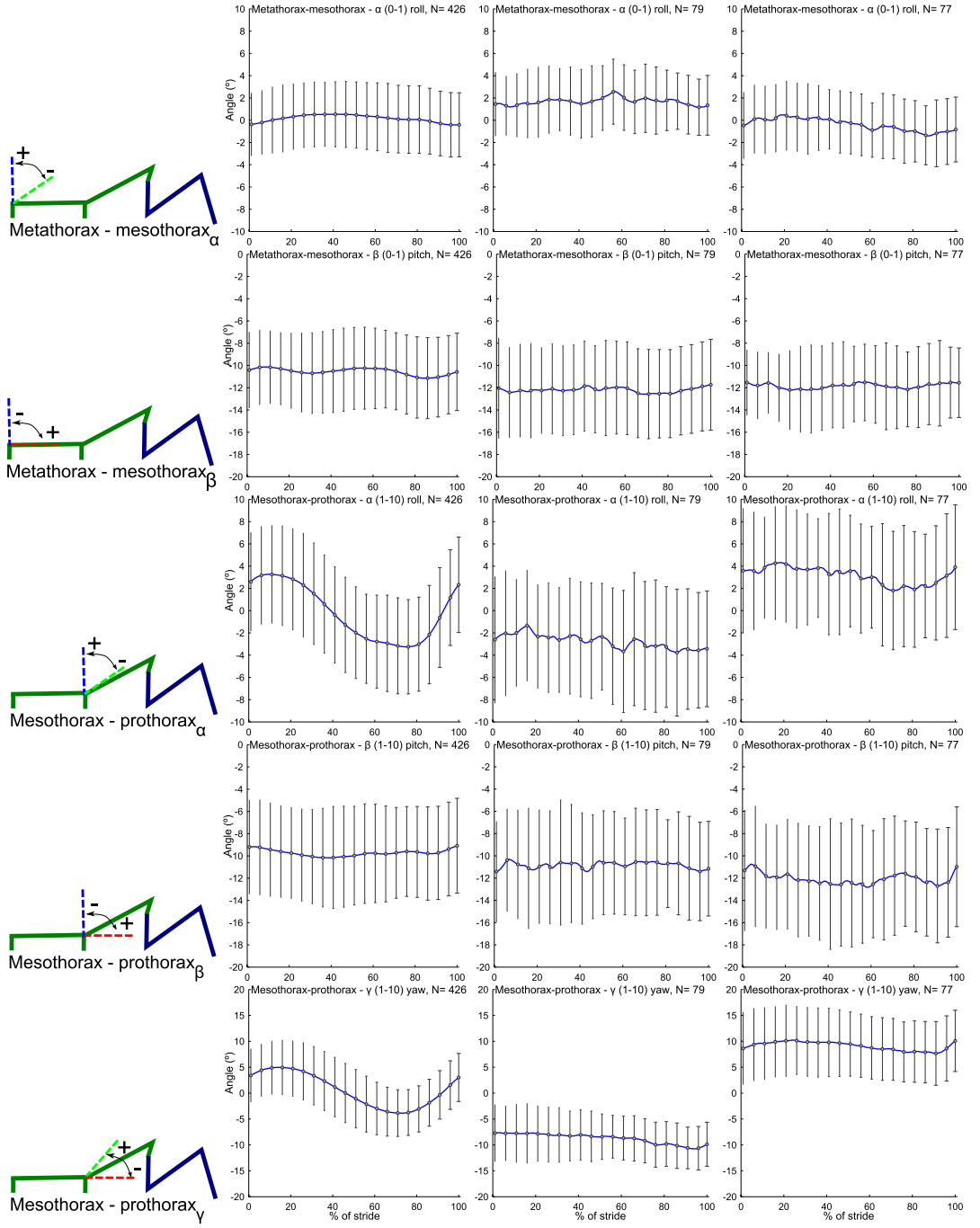


Figure 4.9: Mean, standard deviation of angles values for the thorax and number of samples (N) relative to the stance-swing cycle of the front right leg during forward walking (left), right (middle) and left (right) turn. 0% represents the start of stance and 100% the end of swing.

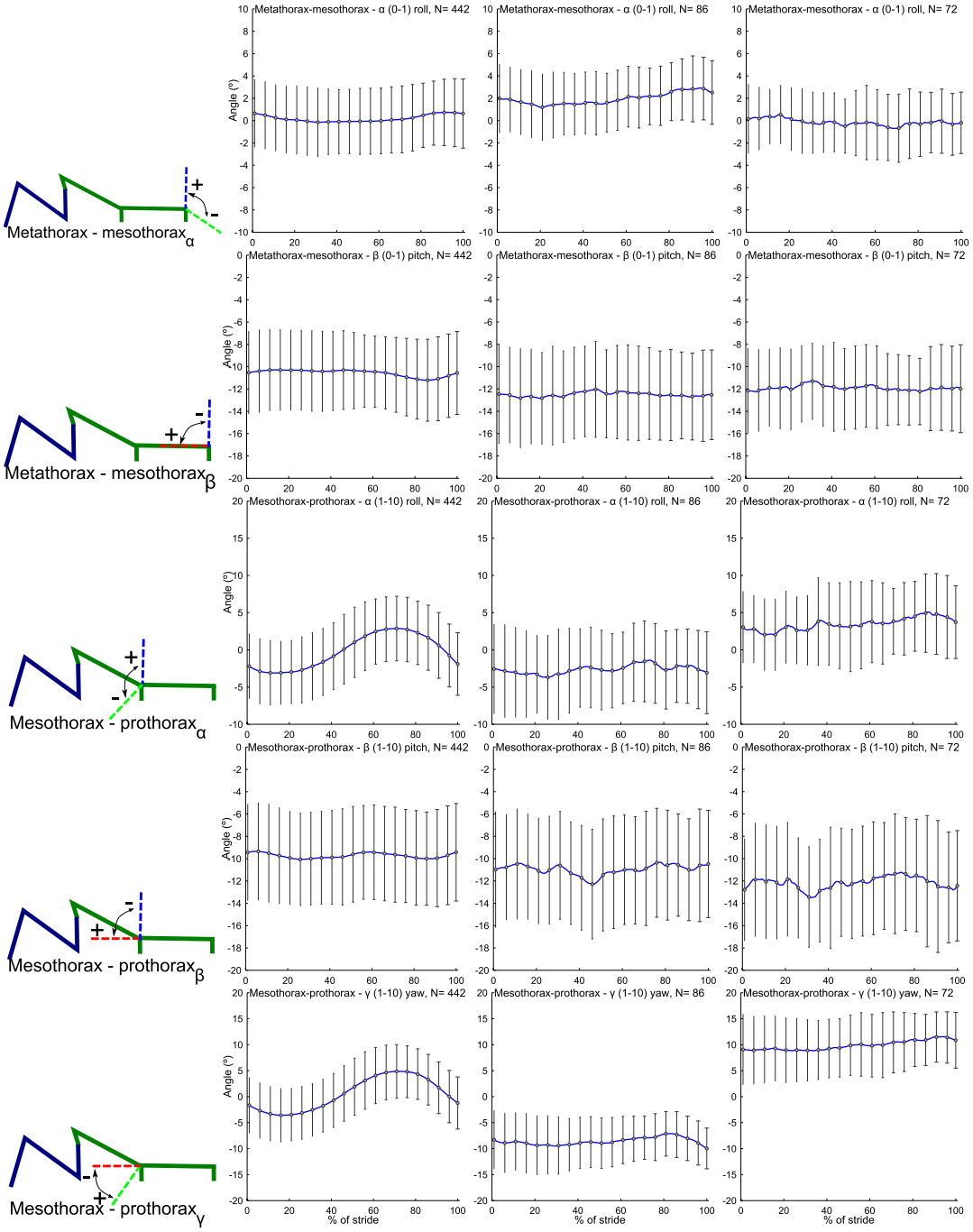


Figure 4.10: Mean, standard deviation of angles values for the thorax and number of samples (N) relative to the stance-swing cycle of the front left leg during forward walking (left), right (middle) and left (right) turn. 0% represents the start of stance and 100% the end of swing.

In order to transition from forward walking to turning there are some joints in each leg that play a crucial role. For the front legs during contralateral turn the freezing of the CTr and FTi joints are the most important, while for the ipsilateral turn reducing the movement of all ThC joints produces inside leg motion (figure 4.11). For the middle legs reversing the movement of FTi and CTr joints and reducing the movement of ThC joints would produce ipsilateral turning, while for the contralateral turning the ThC joints angles would slightly change (figure 4.12). The ThC_{γ} would need to reverse the movement to produce inside turning and have larger range of motion to produce contralateral turning (figure 4.13).

Note here that the contribution of all three DoF in the ThC joint to the leg motion make the results difficult to compare to standard models that reduce this joint movement to one DoF. Note also that crickets are making turns - or rather applying small corrections to their heading direction - during forward walking. This is likely to involve much more subtle changes to joint angles than sharp turns. Another general observation is that the patterns of the angles are not sinusoidal and the change in direction is not necessarily aligned with stance - swing transition. I found no evidence that the walking pattern or any leg angle variation is correlated to sound pattern (results not shown). This was also the result in previous studies using a trackball (Baden and Hedwig, 2008; Witney and Hedwig, 2011). Finally, because of the methodology I used, it is difficult to separate the contribution of muscle activity and the mechanical structure to the pattern of change. Slippery surface setups that decouple the legs between them could provide supplementary data to this method (Gruhn et al., 2006; Bender et al., 2010).

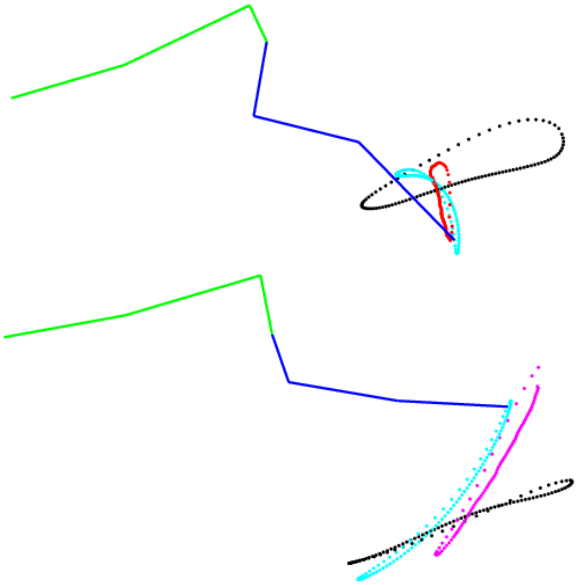


Figure 4.11: Front right leg joints' inside and outside turns contributions. Freezing the motion of all ThC joints at 80% of the step cycle produces similar pattern to ipsilateral turning (top). Freezing the movement of CTr and FTi joints at 80% of the step cycle (appoximately at the beginning of swing) in the forward walking joints values produces similar step pattern to the contralateral turning (bottom). Thorax is depicted with green, leg with blue, forward walking pattern with black, turn pattern with purple and pattern with modified joint angles values with cyan colour.

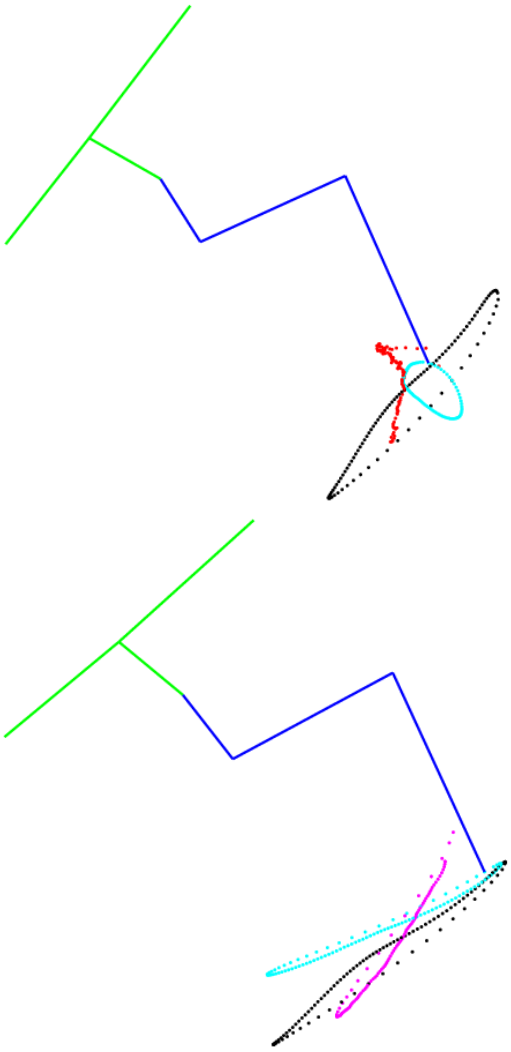


Figure 4.12: Middle right leg joints' inside and outside turns contributions. Freezing the motion of all ThC joints at 80% of the step cycle and reversing the motion of CTr and FTi joints produces similar pattern to ipsilateral turning (top). Freezing the movement of CTr and FTi joints at 80% of the step cycle (appoximately at the beginning of swing) in the forward walking joints values produces similar step pattern to the contralateral turning (bottom). Thorax is depicted with green, leg with blue, forward walking pattern with black, turn pattern with purple and pattern with modified joint angles values with cyan colour.

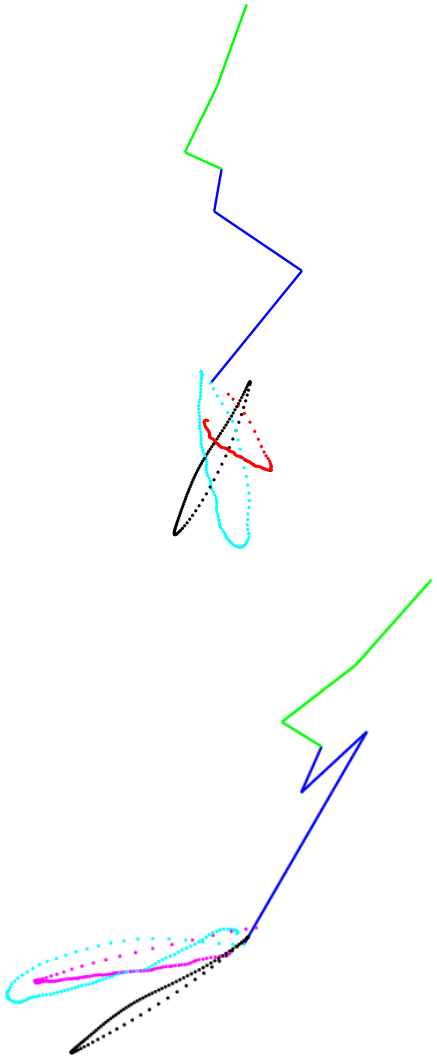


Figure 4.13: Hind right leg joints' inside and outside turns contributions. Altering the movement of the Th_{γ} joint generates smaller movement for the ipsilateral turn (top) and larger movement for the contralateral turn (Bottom). Thorax is depicted with green, leg with blue, forward walking pattern with black, turn pattern with purple and pattern with modified joint angles values with cyan colour.

4.3 Leg Coordination

In this section I address the following questions:

- What is the coordination of leg swing during forward walking and both right and left turns?
- Can the existing coordination rules (Cruse et al., 1991) explain the leg coordination results from the experiments?

During right turning the front left (6 times), middle left (5 times) the hind left (3 times) and front right (3 times), are the first legs to lift off the ground. During left turning the front right leg (5 times), the middle right leg (4 times), the hind right leg (3 times) and the front left (3 times). This is different from results in flies *Ormia ochracea* (Mason et al., 2005) where the ipsilateral front leg, the contralateral front leg and the contralateral mesothoracic leg initiate turning for sounds presented at 90° and 180°.

In order to summarize the steps combinations I gathered the occurrences where one, two or three legs were simultaneously in the swing state (figure 4.14). Each occurrence changed when a different leg combination appeared. It is important to note that in the vast majority of cases two or three legs were never lifted off and touched the ground at precisely the same time (cockroach; Hughes, 1952). Nevertheless, I considered these cases as doublets or triplets.

In forward walking the majority of the stepping combinations occur in doublets, with the following combinations: hind leg with opposite front leg, front leg with opposite middle leg and middle leg with opposite hind leg. In singlet combinations the middle legs are most common. In triplets the front and hind legs of one side and the middle leg of the other side represent the majority of cases.

During right and left turns there are only a few triplet combinations. Most cases happened in singlets where the contralateral to the turn front and middle legs were lifted off the ground. Most doublets represent successive opposite side leg combinations as happened with the forward walking.

There are some step combinations that cannot be explained using the existing coordination rules. For example ipsilateral neighbours should not protract at the same time. However this happened only once in forward walking and twice during turning. More interestingly, contralateral neighbours were more often protracting at the same time. For instance, there were 25 and 9 cases of both middle legs lift off the ground during forward walking and turning, which also violates the standard coordination rules. In

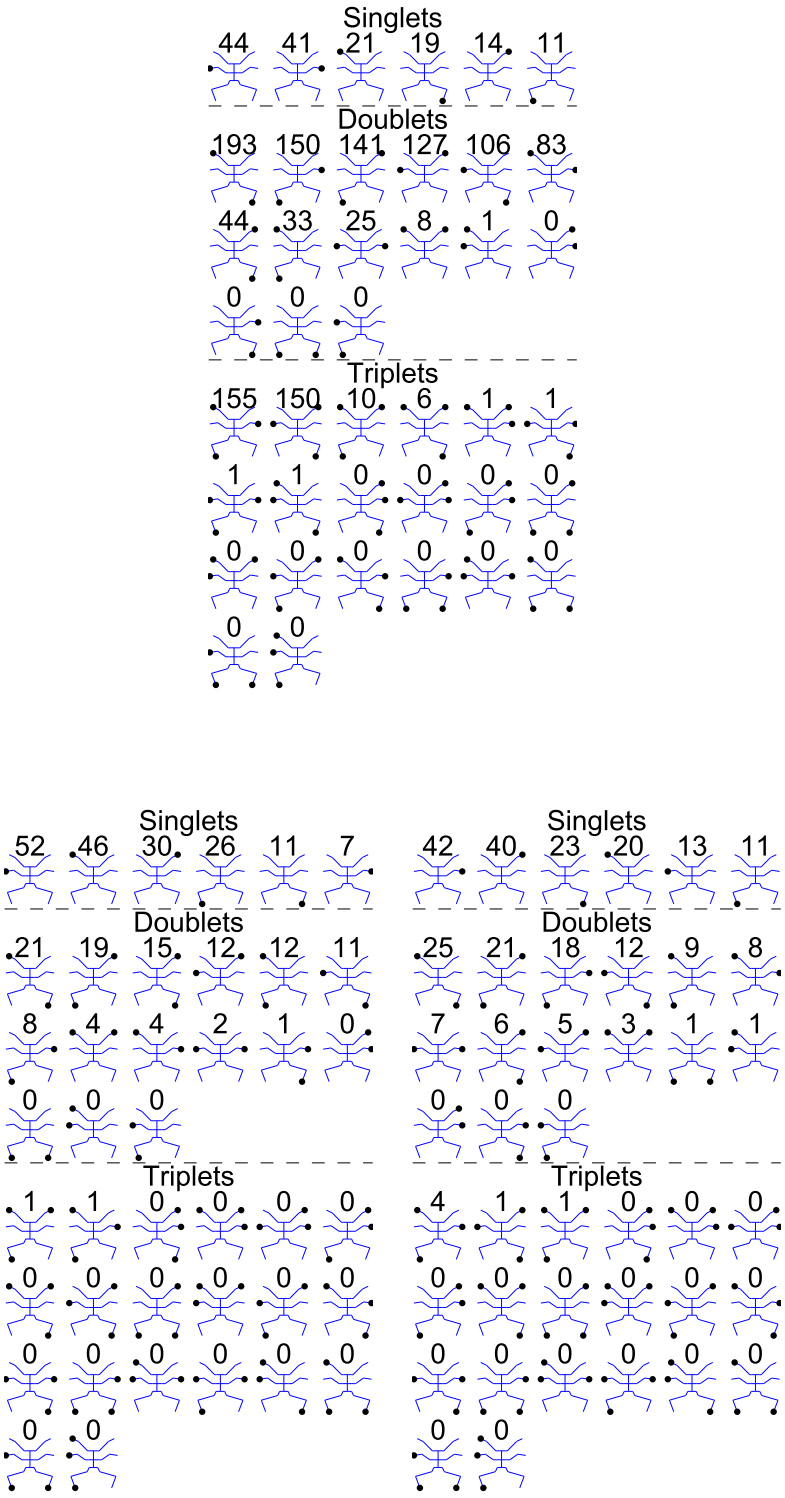


Figure 4.14: Stepping combinations during forward walking (top), right turn (bottom left) and left turn (bottom right). The dots in each case represent legs in swing state.

L	FR	MR	HR	FL	ML	HL
FR	1	21	129	192	71	11
MR	255	2	7	13	82	63
HR	6	179	0	147	17	75
FL	147	102	29	1	43	120
ML	23	56	96	246	0	6
HL	172	11	44	14	181	0

L	FR	MR	HR	FL	ML	HL
FR	0.24	4.94	30.35	45.18	16.71	2.59
MR	60.43	0.47	1.66	3.08	19.43	14.93
HR	1.42	42.22	0.00	34.67	4.01	17.69
FL	33.26	23.08	6.56	0.23	9.73	27.15
ML	5.39	13.11	22.48	57.61	0.00	1.41
HL	40.76	2.61	10.43	3.32	42.89	0.00

Table 4.6: Total number and probability of next steps during forward walking. Left column indicates the leg in swing before and top row the leg in swing after.

L	FR	MR	HR	FL	ML	HL
FR	1	4	7	12	31	19
MR	2	0	6	4	6	4
HR	14	2	2	13	6	14
FL	40	7	11	3	5	17
ML	4	3	9	52	2	2
HL	10	2	2	0	40	2

L	FR	MR	HR	FL	ML	HL
FR	1.35	5.41	9.46	16.22	41.89	25.68
MR	9.09	0.00	27.27	18.18	27.27	18.18
HR	27.45	3.92	3.92	25.49	11.76	27.45
FL	48.19	8.43	13.25	3.61	6.02	20.48
ML	5.56	4.17	12.50	72.22	2.78	2.78
HL	17.86	3.57	3.57	0.00	71.43	3.57

Table 4.7: Total number and probability of next steps during right turn. Left column indicates the leg in swing before and top row the leg in swing after.

particular most of these cases happened towards the end of the turn or the beginning of forward walking. One possible explanation for this is that in these cases both middle legs were extending back reaching almost the limits of their ThC_γ joints. This means that if only one of the legs was lifted of the ground and the insect moved, the other leg could not support the insect as it would have to extend to its full length.

In order to investigate further the influence of each leg to the other legs, I gathered the cases of what is the first leg that enters the swing mode after one leg goes back to its stance mode, for forward walking, right turn and left turn (tables 4.6 - 4.8). These tables provide the number of occurrences and the resulting probability of each leg transitioning to swing state after the other leg transitioned to stance mode.

From all the cases it is clear that the each leg almost never lifts up again before another leg during forward walking and turning. During forward walking the front right leg influences mostly the hind right, front left and middle left legs. The middle right leg affects mostly the front right leg, the middle left leg and the hind left leg. The hind right leg affects mostly the middle right leg, the front left leg and the hind left leg.

L	FR	MR	HR	FL	ML	HL
FR	3	6	24	27	10	6
MR	41	2	4	5	5	17
HR	3	36	1	11	7	3
FL	8	31	13	1	7	10
ML	7	11	6	4	0	7
HL	16	7	16	8	6	0

L	FR	MR	HR	FL	ML	HL
FR	3.95	7.89	31.58	35.53	13.16	7.89
MR	55.41	2.70	5.41	6.76	6.76	22.97
HR	4.92	59.02	1.64	18.03	11.48	4.92
FL	11.43	44.29	18.57	1.43	10.00	14.29
ML	20.00	31.43	17.14	11.43	0.00	20.00
HL	30.19	13.21	30.19	15.09	11.32	0.00

Table 4.8: Total number and probability of next steps during left turn. Left column indicates the leg in swing before and top row the leg in swing after.

The effect of the left legs is opposite as expected. During right turns the front right leg influences mostly the front left, middle left and hind left legs. The middle right leg influences mostly the hind right, front left, middle left and hind left legs. The hind right leg influences mostly the front right, front left, middle left and hind left legs. Again these results do not point towards simple coordination rules in which ground contact of one leg causes transition to swing in a neighbouring leg.

4.4 Angles Relative to Speaker

In this section I address the following questions:

- What are the body and ear angles relative to the sound source?
- At what angle to the sound do crickets stop their initial turn and start walking forward?
- What deviations during forward walking lead to corrections in turning?

Because it was impossible to track the position of the spiracles and the ears, even by using hand digitization, I used a 150 mm digital calliper (Resolution 0.01 mm, Toolzone) to do the necessary measurements after the experiments. Firstly the cricket was sacrificed after experimentation by placing it in a freezer for approximately 30 minutes. The cricket was then removed from the freezer and allowed regain environment temperature. After that, I used the calliper to measure the distance of the ears from the front FTi joints. This was measured as 1.0 ± 0.1 mm for all 16 specimens. The position of the spiracles was approximated by measuring the distances of three successive rotations following the model order of rotations from the mesothorax joint. These

measurements were stored at a vector where x = 2.5 mm, y = 2.0 mm and z=0.5 mm, where all the rotations are 90°.

I calculated three types of angles relative to the speaker (figure 4.16). I took the 2D projection to the ground of the 3D coordinates of each point of interest. The first is the angle between the metathorax, the mesothorax and the centre of the speaker. The second is the angle between the mesothorax, the prothorax and the centre of the speaker. For the third angle I created a segment connecting the two ears. I then calculated the centre of the segment and created a second segment vertical to the previous one. Therefore the third angle I calculated is the one between the tip of the second segment, the middle of the ears's segment and the centre of the speaker (see figure 4.16). Note that this is actually the most relevant measure but almost never reported in previous studies. 180° is the angle where the cricket is perfectly aligned with the speaker. There are cases when the cricket turned to the other direction than it should but eventually finished the turn oriented towards the speaker. Therefore there are cases where the angle relative to the speaker are less than 0° or more than 360°. Table 4.9 summarizes the results and figure 4.15 depicts the results of the ears - speaker angle in two examples. In the first the cricket finished its turn very precisely while in the other the insect continued turning after crossing the alignment with the speaker. Note that these are two different specimens. Some of the crickets were able to track the sound source more accurately than others. Note also that the oscillations observed in the angles are due to the stepping cycles of the front legs.

Maximum difference with the speaker alignment at the beginning of the turn was 224.48° for the metathorax-mesothorax-speaker angle, 217.77° for the mesothorax-prothorax-speaker angle and 217.36° for the ears-speaker angle. Minimum difference with the speaker alignment at the beginning of the turn was 32.69° for the metathorax-mesothorax-speaker angle, 28.91° for the mesothorax-prothorax-speaker angle and 37.73° for the ears-speaker angle. Maximum difference with the speaker alignment at the end of the turn was 73.07° for the metathorax-mesothorax-speaker angle, 67.12° for the mesothorax-prothorax-speaker angle and 80.10° for the ears-speaker angle. Minimum difference with the speaker alignment at the beginning of the turn was 0.58° for the metathorax-mesothorax-speaker angle, 0.31° for the mesothorax-prothorax-speaker angle and 0.49° for the ears-speaker angle. Mean difference with the speaker alignment at the beginning of the turn was 132.89° ±43.85° for the metathorax-mesothorax-speaker angle, 131.49° ±44.90° for the mesothorax-prothorax-speaker angle and 130.73° ±43.80° for the ears-speaker angle. Mean difference with the speaker alignment at the

end of the turn was 17.31° ±17.37° for the metathorax-mesothorax-speaker angle, 17.07° ±17.47° for the mesothorax-prothorax-speaker angle and 19.91° ±19.45° for the ears-speaker angle.

In order to investigate the change of direction during forward walking I gathered the peaks of the angles relative to the speaker during forward walking from all the 16 experiments (figure 4.17). I used MATLAB's findpeaks function with minimum time difference between successive peaks equal to 1 second. Maximum value of angle difference for the mesothorax-metathorax-speaker was 53.49°, for the mesothorax-prothorax-speaker was 62.57° and for the ears-speaker was 82.86°. Minimum value of angle difference for the mesothorax-metathorax-speaker was 0.57°, for the mesothorax-prothorax-speaker was 0.26° and for the ears-speaker was 0.34°. Mean value of angle difference was 16.24° ±11.62° for mesothorax-metathorax-speaker, 18.34° ±13.54° for mesothorax-prothorax-speaker and 28.48° ±16.04° for the ears-speaker. The results were summarized by using histograms with a bin size of 5° (figure 4.17).

Overall the results show that the crickets after the initial turn approach the calling song meandering around the straight target direction. Earlier studies on a Kramer treadmill resulted in deviation from the straight path of the insect around 30°-60° (Weber et al. 1981, *Gryllus campestris*; Schmitz et al. 1982). Here I showed that most of these deviations were lower than 30°. One possible reason for this is that forces generated while walking on a Kramer treadmill are opposing the acceleration of the insect, thus altering sensory feedback. More recently it was showed that crickets can discriminate sound deviating by only 1° (Schöneich and Hedwig, 2010). However, thosse experiments were conducted on a trackball where the moving animal did not alter the orientation and direction towards the sound and sound was constantly perceived under identical conditions. In noisier environments such as in the arena this precision in tracking the sound is probably less accurate. Another difference with previous studies is that there is course correction while the cricket is moving in contrast to results from other species (*Scapsipedus marginatus*; Murphey and Zaretsky 1972, *Teleogryllus oceanicus*; Bailey and Thomson 1977) where there is course correction after a stop.

C	E	S	T	MMSI	MMSA	MPSI	MPSA	VMSI	VMSA
01	01	R	R	331.04°	205.83°	330.35°	199.41°	335.33°	190.75°
01	02	L	R	212.71°	186.63°	207.81°	182.98°	217.02°	187.10°
02	01	L	L	23.68°	180.25°	19.86°	191.76°	20.41°	181.81°
02	02	R	L	38.52°	161.11°	49.24°	175.49°	45.75°	189.49°
03	01	R	R	259.38°	204.38°	261.22°	191.49°	249.80°	189.62°
03	02	L	R	252.81°	183.46°	253.65°	173.93°	256.82°	174.33°
04	01	R	R	282.41°	196.66°	265.57°	179.13°	263.38°	167.21°
04	02	L	L	97.75°	161.79°	92.03°	166.09°	89.23°	170.18°
05	01	R	R	365.33°	197.96°	365.57°	193.73°	353.21°	202.89°
05	02	L	L	-12.39°	177.89°	-17.57°	194.64°	-8.96°	195.53°
06	01	R	R	351.13°	137.42°	356.51°	123.56°	355.09°	126.87°
06	02	L	L	56.52°	159.06°	66.86°	173.47°	74.86°	168.32°
07	01	R	L	22.46°	110.63°	33.12°	118.13°	27.40°	99.94°
07	02	L	R	282.30°	177.01°	279.43°	170.63°	279.98°	183.55°
08	01	R	R	346.29°	169.47°	354.31°	162.93°	361.91°	146.01°
08	02	L	R	337.23°	195.25°	337.97°	176.37°	332.04°	168.49°
09	01	L	R	328.70°	166.83°	332.55°	157.40°	327.59°	160.58°
09	02	R	L	-4.21°	169.90°	2.76°	180.88°	0.48°	191.80°
10	01	L	L	81.97°	201.03°	91.83°	211.73°	95.61°	215.75°
10	02	R	R	295.60°	197.56°	282.96°	181.21°	289.58°	179.43°
11	01	R	R	324.84°	169.42°	328.72°	157.67°	332.16°	149.78°
11	02	R	L	9.28°	183.47°	11.18°	191.19°	11.54°	192.51°
12	01	R	L	98.90°	178.82°	98.33°	185.10°	87.77°	181.23°
12	02	R	L	-5.73°	192.85°	-0.41°	205.46°	1.94°	219.33°
13	01	L	L	17.88°	158.71°	16.16°	160.12°	22.11°	145.57°
13	02	R	L	76.81°	213.81°	80.57°	222.67°	80.46°	227.09°
14	01	R	R	335.74°	177.34°	345.09°	170.90°	345.48°	174.74°
14	02	R	R	404.25°	201.30°	397.72°	193.10°	397.26°	200.10°
15	01	R	L	81.62°	181.11°	74.32°	181.41°	89.22°	175.36°
15	02	L	L	48.94°	107.91°	48.97°	112.37°	55.26°	118.08°
16	01	L	R	277.41°	190.98°	278.59°	182.57°	274.51°	189.19°
16	02	R	R	255.55°	168.72°	254.58°	168.54°	263.80°	178.98°

Table 4.9: Angles properties for all the experiments. Cricket number (C), experiment number (E), speaker(S), left (L), right (R), turn(T), metathorax - mesothorax - speaker initial angle (MMSI) and after turn(MMSA), mesothorax - prothorax - speaker initial angle (MPSI) and after turn (MPSA), vertical line ears point - middle ears point - speaker initial angle (VMSA) and after turn (VMSA) and antennae and head movement frames before first leg swing (AM).

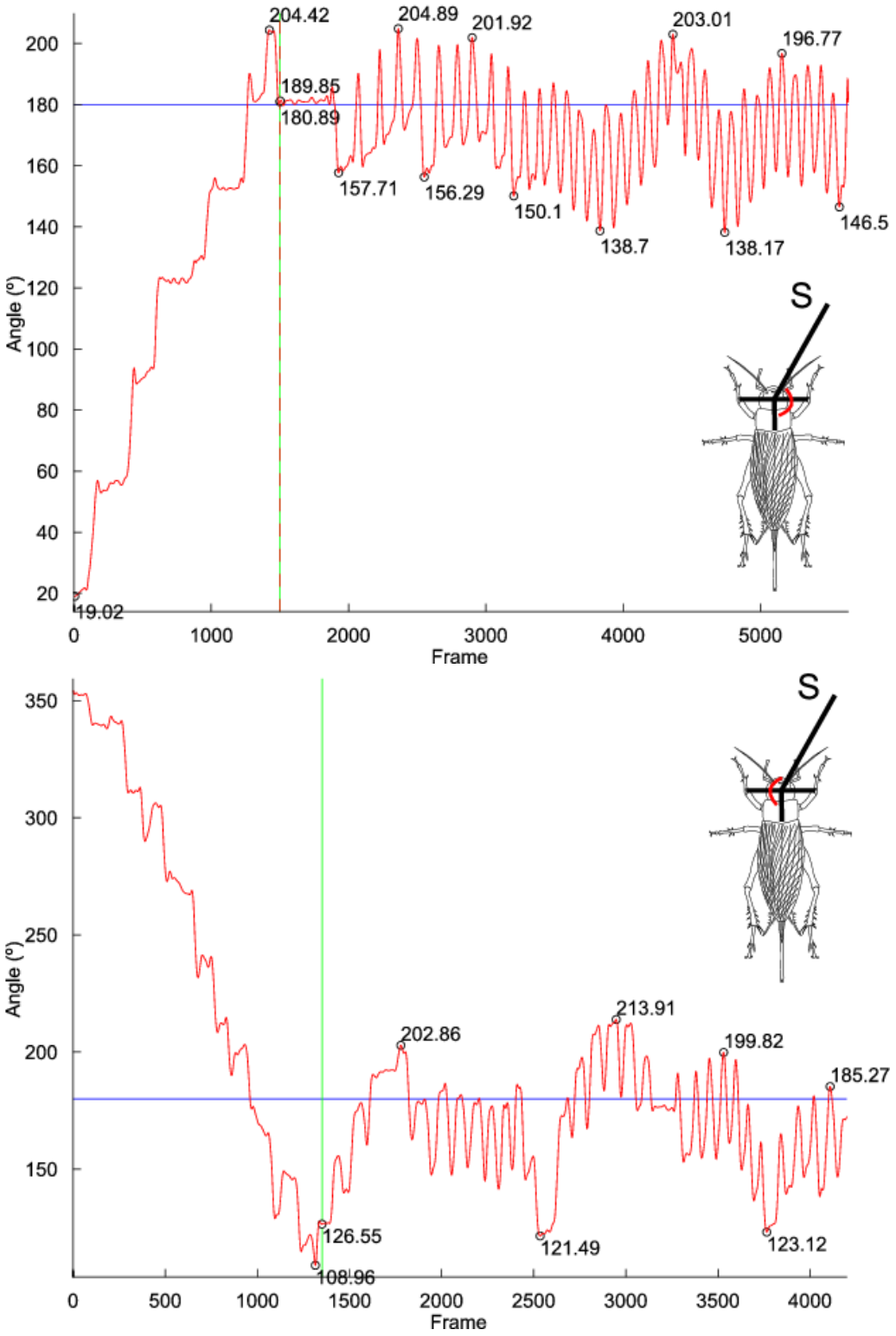


Figure 4.15: Examples of angles between the ears and the speakers (S). Top figure shows results from a cricket that tracked the sound very precisely. Bottom figure shows results from a cricket that continued turning but corrected its course. Green lines indicate the end of turn. Dashed red lines indicate a stop.

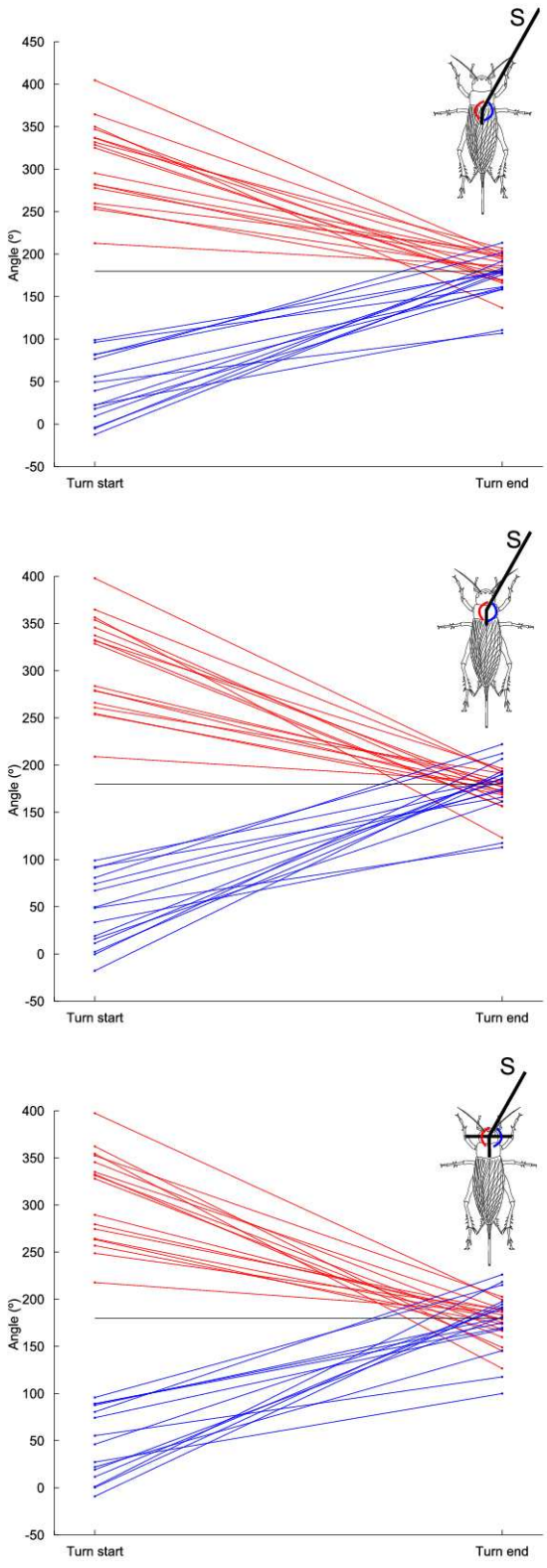


Figure 4.16: Summary of the angles of interest relative to the speakers (S). Top figure summarizes the angles between metathorax, mesothorax and the speaker. Middle figure summarizes the angles between mesothorax, prothorax and the speaker. Bottom figure summarizes the angles between the ears' lines and the speaker. Right turns are marked with red colour and left turns are marked with blue colour.

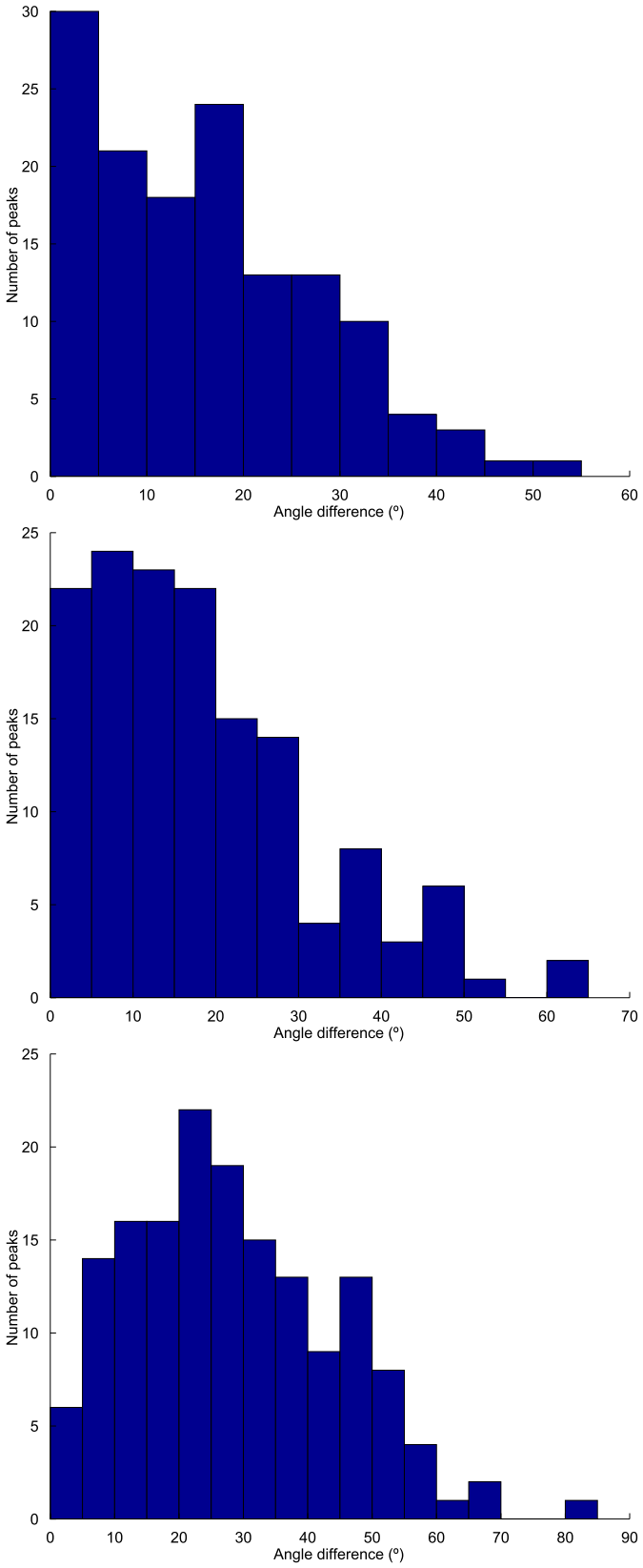


Figure 4.17: Angles before change of direction during forward walking. Number of peaks in the metathorax-mesothorax-speaker angles (Top). Number of peaks in the mesothorax-prothorax-speaker angles (Middle). Number of peaks in the ears-speaker angles (Bottom).

4.5 Ears' Input Estimation

In this section I address the following question:

- What is the sound input from each side of the cricket during phonotaxis?

In order to test the parameters of the estimation algorithm I first created a simulated stationary cricket setup. This is similar to the setup that was used to calculate the delays and gains of transmitting the sound to real crickets (Michelsen et al., 1994). The gains represent the change of amplitude and the delays in the phase angles from the entrance of the tracheal system to the surface of the tympanum.

I placed a simulated cricket in the middle of a circular arena and rotated the speaker around the right tympanum one degree every one millisecond (figure 4.18). In the original paper the speaker was moved every 30°. The distance from the speaker in my simulation was 400mm. The lengths of the cricket segments are based on the mean values from the estimated lengths from all the crickets that were tracked (table 4.10). The angle values are based on the forward walking stride percentage results that were depicted in section 4.2. The distance between the two tympani was 12.08 mm, the distance between each spiracle and the contralateral tympanum was 9.85 mm, the distance between the each spiracle and the ipsilateral ear was 6.98 mm and the distance between the two spiracles was 4 mm. For the calculations I consider that there is only one tympanum per side and it is placed in the line connecting the FTi with the TiTa joints.

For the calculation of the ear input I used all four sound inputs. These are the ipsilateral tympanum (IT), the ipsilateral spiracle (IS), the contralateral spiracle (CS) and the contralateral tympanum (CT). According to Michelsen et al. (1994) at carrier frequency of 4.5 kHz the contribution of the CT input to the sound is not significant. However, at 4.8 kHz, which is the carrier frequency I used in my experiments, the CT input affects significantly the directionality. This is supported by experiments where the contralateral tympanum was blocked (Boyd and Lewis, 1983). This fact was not taken into account in previous 2D simulations of the model (Reeve et al., 2007). The internal delays and the sound gains for each spiracle and tympani are based on (Michelsen et al., 1994) and data provided by Axel Michelsen (personal communication). These values are presented in table 4.12. Because of the way these values were originally calculated, I had to convert them before using them in the algorithm. Excluding the IT internal delay, which is zero by default, the other values had to be transformed by subtracting them from 180°. If the value is negative then an addition of

Segment	**MV**	**SD**
Metahorax - mesothorax (0 - 1)	3.05	±0.23
Mesothorax - thorax-coxa (1 - 2, 1 - 6)	1.86	±0.11
Middle coxa (2 - 3, 6 - 7)	1.59	±0.17
Middle femur (3 - 4, 7 - 8)	5.29	±0.32
Middle tibia (4 - 5, 8 - 9)	4.33	±0.22
Mesothorax - prothorax (1 - 10)	3.58	±0.31
Prothorax - thorax - coxa (10 - 11, 10 - 15)	1.56	±0.16
Front coxa (11 - 12, 15 - 16)	2.01	±0.34
Front femur (12 - 13, 16 - 17)	5.50	±0.30
Front tibia (13 - 14, 17 - 18)	3.54	±0.24
Metathorax - thorax - coxa (0 - 19, 0 - 23)	1.68	±0.14
Hind coxa (19 - 20, 23 - 24)	1.82	±0.17
Hind femur (20 - 21, 24 - 25)	10.50	±0.44
Hind tibia (21 - 22, 25 - 26)	7.98	±0.38

Table 4.10: Mean values (MV) and standard deviations (SD) for the lengths of body and leg segments in millimetres.

360° needed to be made to make the values positive. Note that I used the same values for all the crickets. According to Michelsen et al. (1994) the diffraction and time delays did not vary much between individuals. In contrast, the gains between individuals showed substantial variation. Furthermore, differences in the gains between the two sides in the same cricket were found.

I did not take into account diffractions of the sound, as this was not possible to calculate. Michelsen et al. (1994) estimated a diffraction of 1-2 dB. As I wanted to estimate the input from an analogue signal I used a sample rate of 8×10^6 Hz instead of 44.1 kHz used in the experiments. By using this sample rate I then used the index of the song to estimate the input by using the following procedure: first at every millisecond the sound is broadcast at time t. Then the sound reaching each of the two tympani and the spiracles must be at the time $t - t_p$ where the t_p is the time taken to reach the specific point from the sound source. To calculate this time I used a speed of sound time value of 344,384 m/s or mm/ms. This value is for an air temperature of 22°C, the average temperature during the arena experiments. Therefore the time taken for the signal to travel was taken by the distance of the point from the sound source divided by the speed of sound. Then, this value was added to the internal delays multiplied

Joint	**Parameters**	**Values**
Metathorax (0)	*x*, *y*, *z*	0, 0, 0
Segment	**Parameters**	**Values**
Metahorax - mesothorax (0 - 1)	α, β, γ	0°, -10°, 0°
Middle right coxa (2 - 3)	α, β, γ (ThC)	-25°, 30°, 0°
Middle right femur (3 - 4)	β (CTr)	-80°
Middle right tibia (4 - 5)	β (FTi)	95°
Middle left coxa (6 - 7)	α, β, γ (ThC)	25°, 30°, 0°
Middle left femur (7 - 8)	β (CTr)	-80°
Middle left tibia (8 - 9)	β (FTi)	95°
Mesothorax - prothorax (1 - 10)	α, β, γ	0°, -10°, 0°
Front right coxa (11 - 12)	α, β, γ (ThC)	-45°, 80°, -15°
Front right femur (12 - 13)	α (TrF), β (CTr)	45°, -95
Front right tibia (13 - 14)	β (FTi)	65
Front left coxa (15 - 16)	α, β, γ (ThC)	45°, 80°, 15°
Front left femur (16 - 17)	α (TrF), β (CTr)	−45°, -95°
Front left tibia (17 - 18)	β (FTi)	65°
Hind right coxa (19 - 20)	α, β, γ (ThC)	-8°, 30°, -65°
Hind right femur (20 - 21)	β (CTr)	-70°
Hind right tibia (21 - 22)	β (FTi)	130°
Hind left coxa (23 - 24)	α, β, γ (ThC)	8°, 30°, 65°
Hind left femur (24 - 25)	β (CTr)	-70°
Hind left tibia (25 - 26)	β (FTi)	130°

Table 4.11: The joints and segments parameters values used in the stationary cricket setup. The units for the joint limits are in millimetres and for the angles in degrees.

Input	**Gain**	**Delay**	**180 - delay**	**Final delay**
IT	1.0	0°	0°	0°
IS	-1.44	135°	45°	45°
CS	-0.54	230°	-50°	130°
CT	-0.23	270°	-90°	90°

Table 4.12: Transmission gains and internal delays of the four sound inputs. Ipsilateral tympanum (IT), ipsilateral spiracle (IS), contralateral spiracle (CS) and contralateral tympanum (CT). The internal delays represent the phase difference in the time of the sound arrival as it travels inside the tracheal tubes.

by the degree of sound change which is given by $\frac{1}{360 \times carrierFrequency} \times 1000$. Then from all the samples I took the maximum value, which represents the size of tympanal vibration. The results of this simulation are provided in figure 4.18 and show the clear directionality of the sound for both sides as the speaker is rotated around the cricket.

Before applying the algorithm to the data I also investigated the estimation of the ears input in the stationary setup while the insect is moving its front legs (figure 4.19). For the simulation I used the data gathered for the step cycle as presented in section 4.2. Each frame corresponds to 3 ms. I chose the position of the speaker to be where the maximum difference was observed in the previous experiment (270°). Because in this simulation the legs were moving, I placed the speaker at 270° relative to the metathorax position. First, I calculated the difference between the two sides when the simulated cricket walked forward. When the front right leg initially performs its swing there is a decrease in the difference of the two sides and then an increase as the leg transitions to the stance and the front left leg to its swing. The next case was when the legs performed a left turn and therefore moving away from the speaker. There is a decrease in the difference as the front right leg is in swing, an increase before decreasing again as the leg changes into stance and finally an increase as the front left leg enters its stance. The last case was when the legs would perform a right turn. Initially, there would be an increase as the right leg would move closer to the sound source and a decrease as it would go back to stance, coupled with an increase as the front left leg would perform a swing and a decrease when it would finish its swing. From all the above cases it is obvious that during a step cycle the ears input on the two sides is not constant but instead significantly changed. It important to note that only the legs are moving at this situation and not the body, which means that this experiment resembles more the case when the cricket is walking on a trackball.

If the sound is placed directly in front of the cricket there is smaller difference between the two sides (figure 4.20). During the swing phase of each leg the difference reaches up to 3 dB, while during stance it reaches up to 4 dB. This suggests that the cricket should ignore differences of 4 dB. Alternatively the cricket may be influenced by the change of input during step, *e.g* it could detect that there is an increasing difference during ipsilateral swing if turning to the wrong way (figure 4.19 top, middle), whereas during a turn towards the sound the difference decreases sharply during the swing (figure 4.19 bottom).

In order to calculate the two sides input from the video recordings I first resampled the metathorax coordinates and the angles of all joints from 3.33 ms to 1 ms using

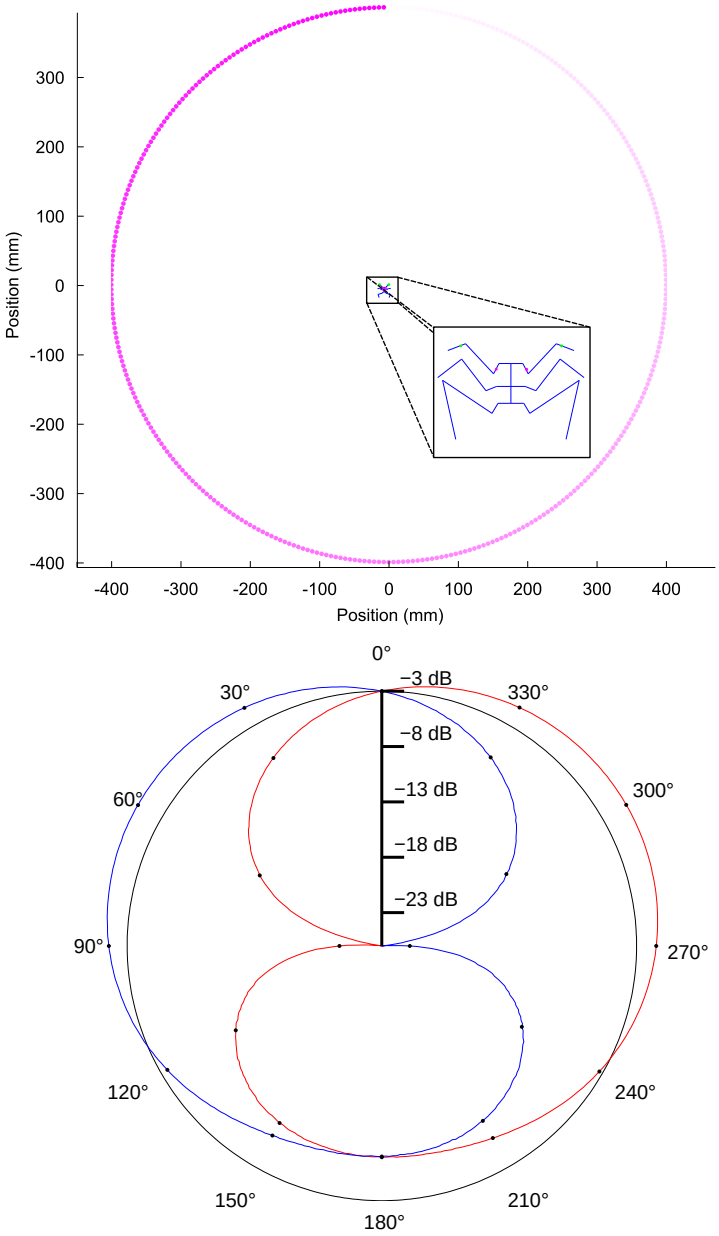


Figure 4.18: Simulation of sound directionality for a stationary cricket. The artificial cricket is placed in the middle of the arena (top). The sound source is rotated around the right tympanum every 1°. The algorithm calculates the values of the sound input for the left (blue) and the right (red) ear. Directional pattern of ear values with respect to the 0° value is presented (bottom).

cubic spline interpolation. Then, I regenerated the coordinates of all the joints, the ears and the spiracles using the same rotation order that I used during the tracking

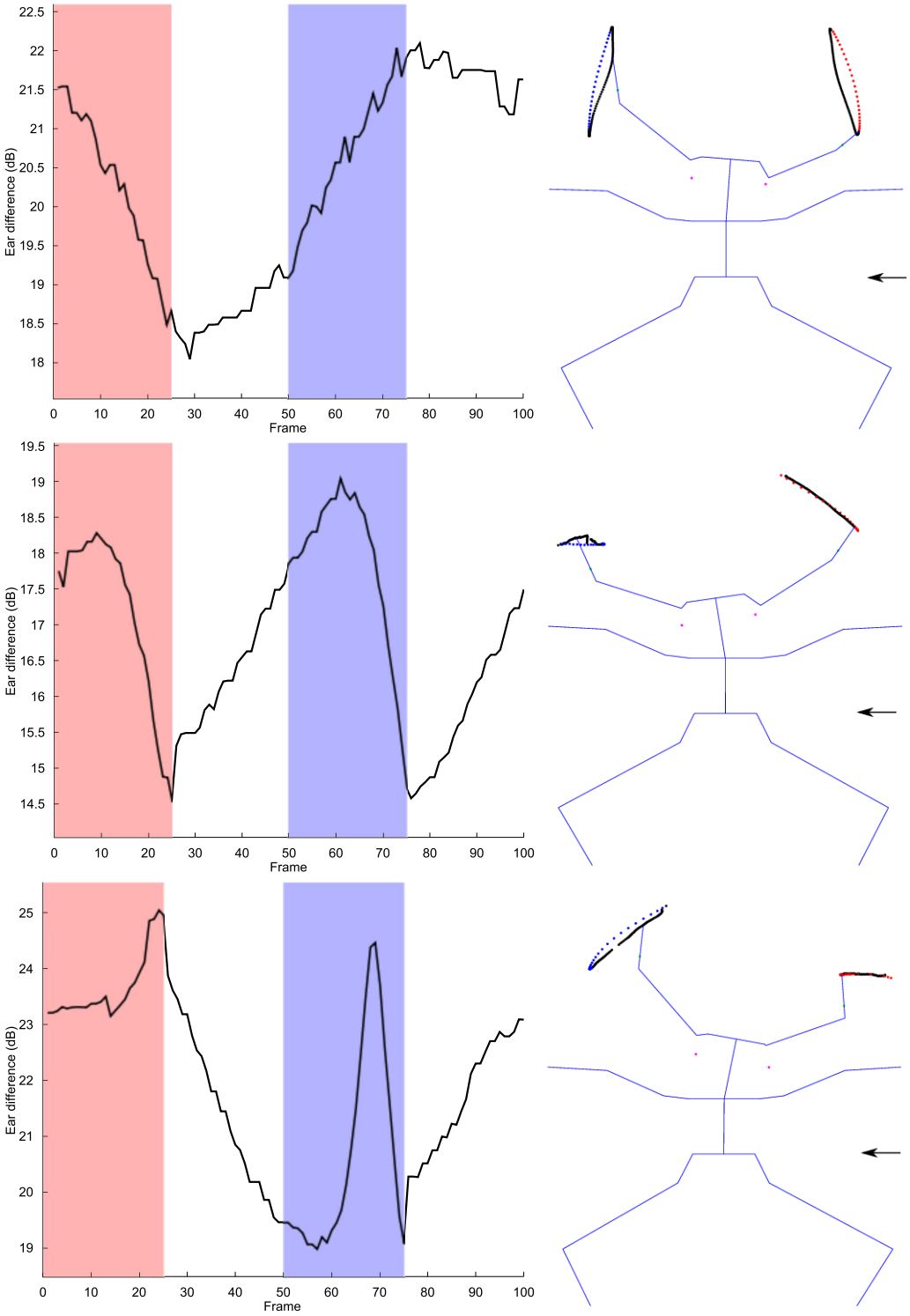


Figure 4.19: Single step cycle decibel difference between the two sides in three different cases. During forward walking (top), during left turn (middle) and during right turn (bottom). The arrow indicates the direction of the sound. Rectangles represent swing phases for front right (light red) and left (light blue) legs.

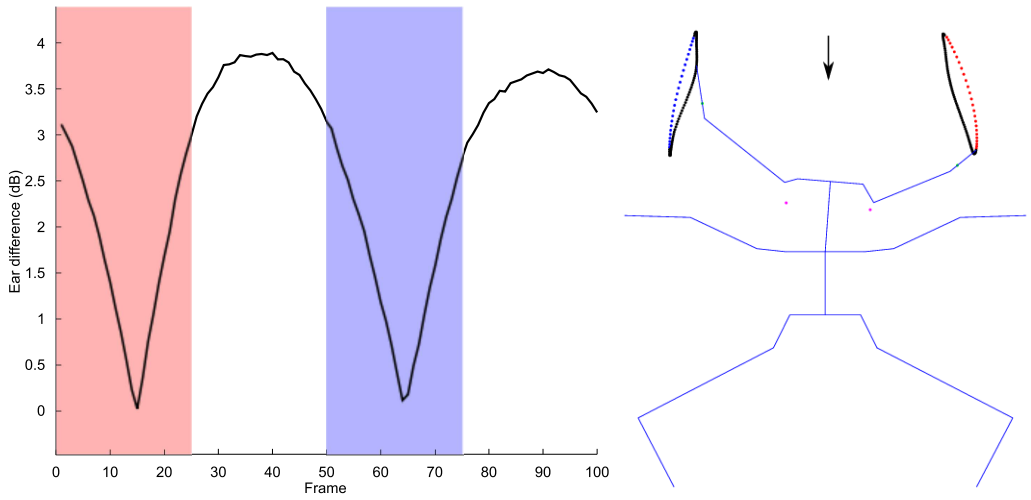


Figure 4.20: Single step cycle decibel difference between the two sides during forward walking. The arrow indicates the direction of the sound. Rectangles represent swing phases for front right (light red) and left (light blue) legs.

procedure. Because the original results were based on 300 fps video recordings, I had to find the delay of the cricket song when the coordinates were resampled. In order to do that I cross correlated the two signals using the MATLAB xcorr function. This function outputs the delay between the two signals and therefore I was able to extract the initial song position at the first frame. Then for every millisecond I calculated the distance from the centre of the speaker. The centre of the left speaker was in X: 290 mm, Y: 1200 mm and Z: 100 mm and the right speaker at X: 290 mm, Y: 0mm and Z: 100 mm. These measurements were done by using a ruler. Figures 4.21 and 4.22 depict typical examples of the estimation of ears input.

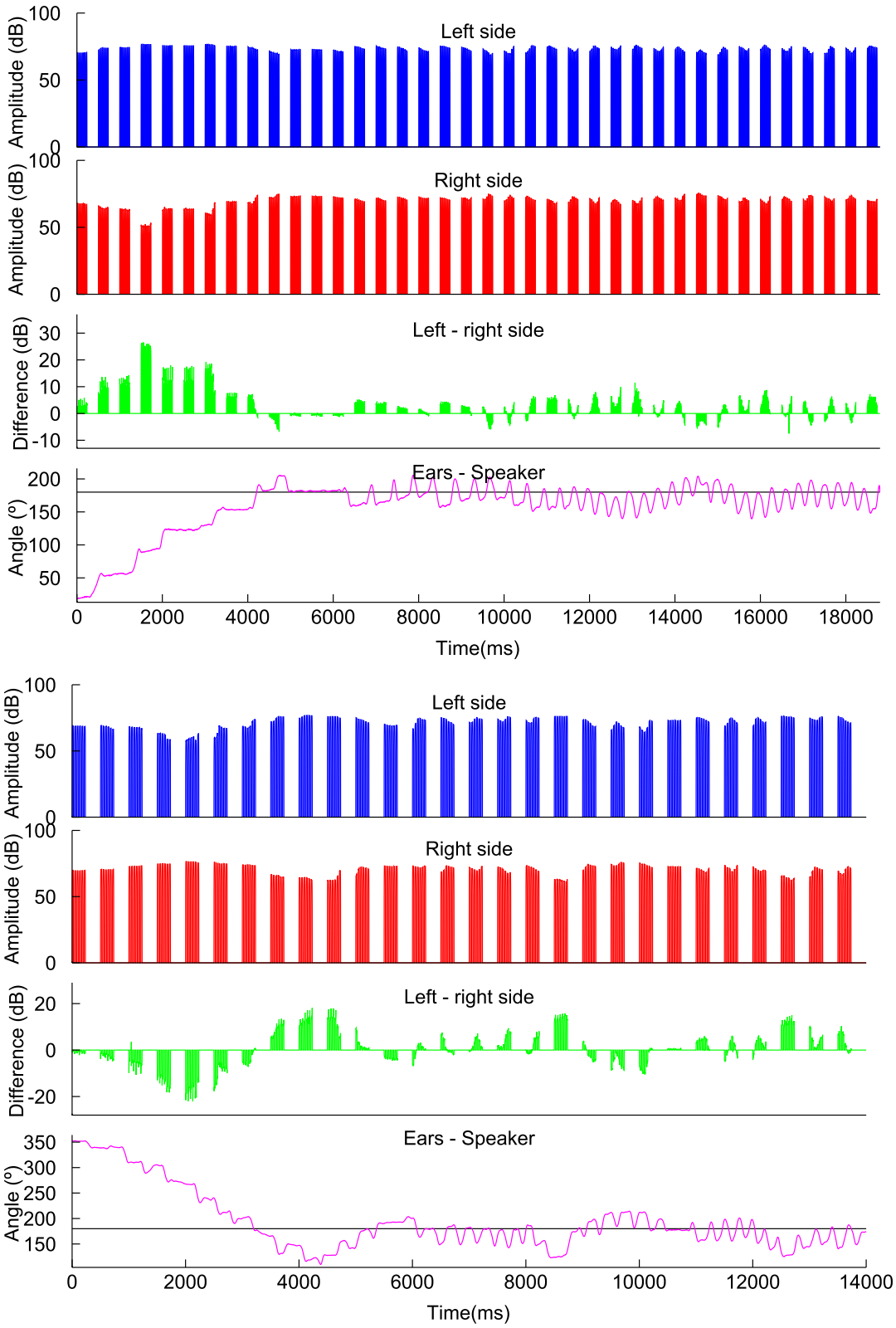


Figure 4.21: Examples of ear's input estimation. Top figure shows results from a cricket that tracked the sound very precisely. Bottom figure shows results from a cricket that continued turning but corrected its course.

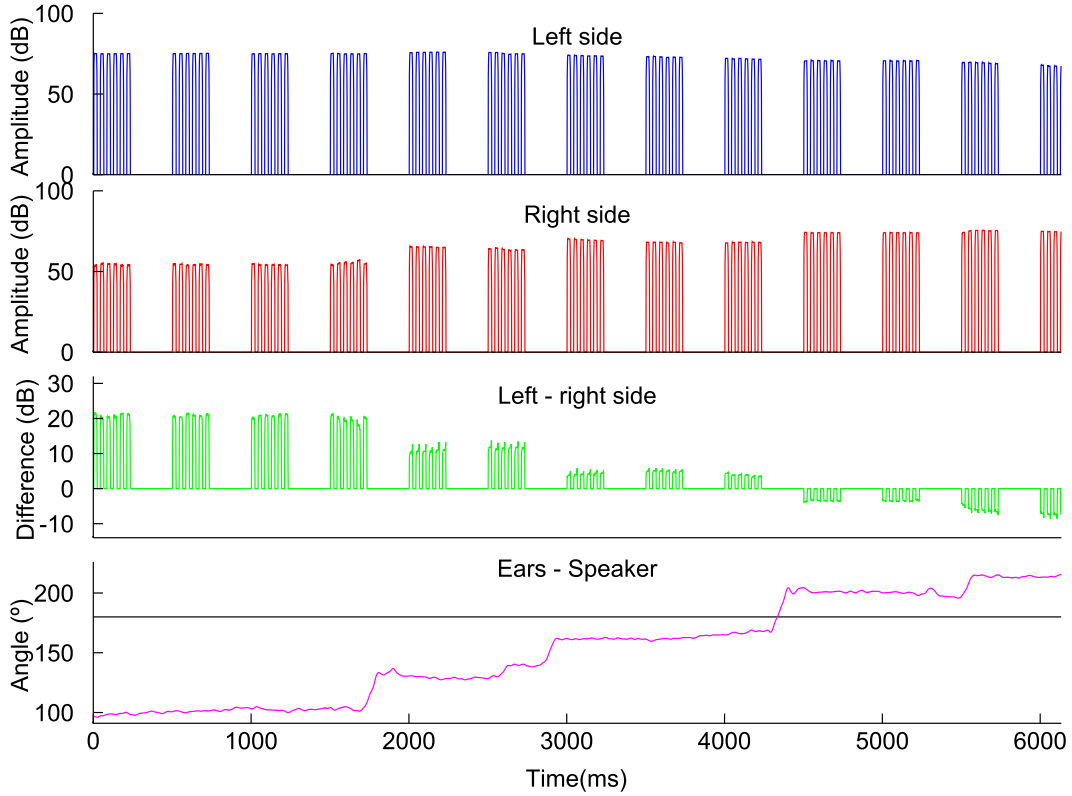


Figure 4.22: Example of ear's input estimation during turn. The cricket performed a left turn towards the left speaker.

Finally, I summarized the results by calculating the maximum input value before the angles' peaks presented in the previous section (figure 4.23). I used a period of 300 ms based on the step cycle of the insect but shifted 50 ms before the peak as this is the estimated time that the cricket takes to process the sound input through the brain (Baden and Hedwig, 2008). Maximum value of decibel difference for the mesothorax-metathorax-speaker was 15.83 dB, for the mesothorax-prothorax-speaker was 22.21 dB and for the ears-speaker was 18.11 dB. Minimum value of angle difference for the mesothorax-metathorax-speaker was 1.04 dB, for the mesothorax-prothorax-speaker was 0.69 dB and for the ears-speaker was 0.53 dB. Mean value of decibel difference was 6.06 $\pm$3.39 dB for mesothorax-metathorax-speaker, 6.47 $\pm$3.95 dB for mesothorax-prothorax-speaker and 5.85 $\pm$3.54 dB for the ears-speaker. Maximum value of decibel difference before the transition from turning to forward walking was 19.17 dB and minimum difference was 7.76 dB. Mean value of decibel difference was 13.17 dB $\pm$ 8.5 dB. These results suggest that the crickets require a difference of 3-5 dB to cause a course correction, which is far from precise and that quite large differences can be tolerated.

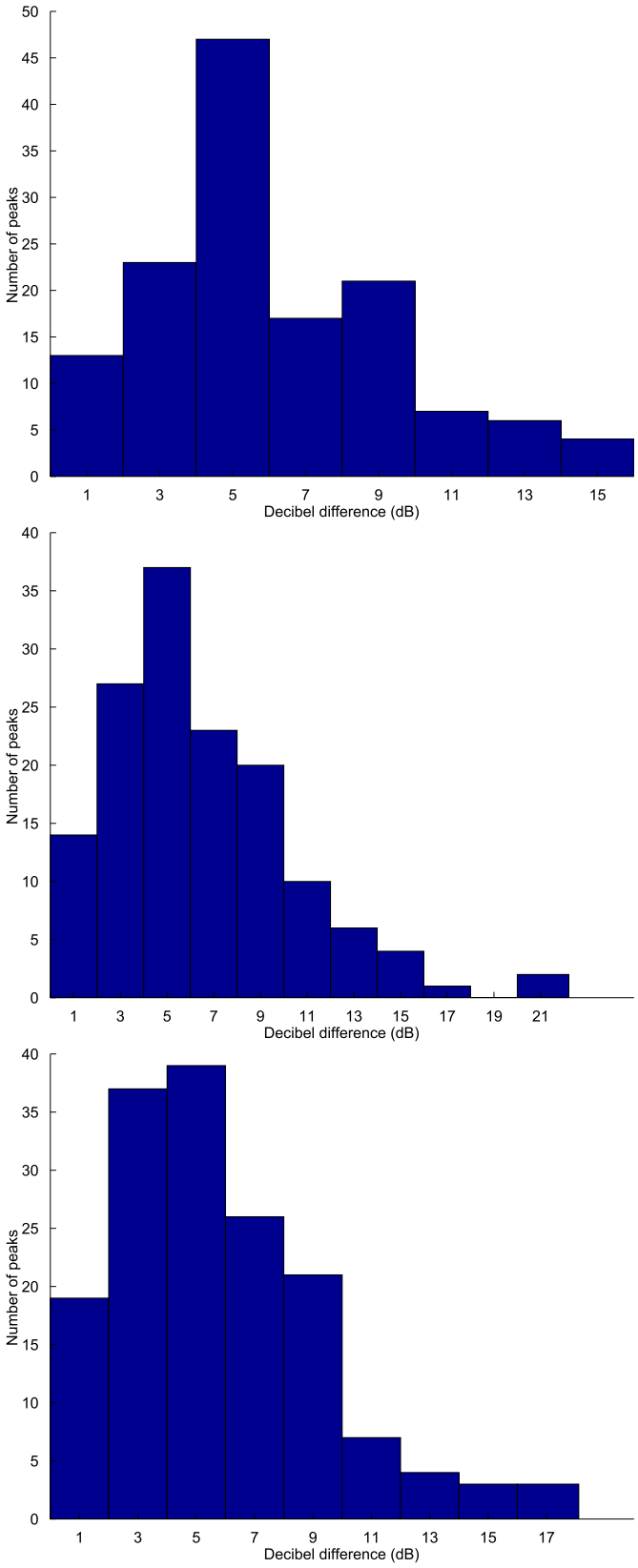


Figure 4.23: Decibel values in the angles peaks before change of direction during forward walking. Number of peaks in the metathorax-mesothorax-speaker angles (Top). Number of peaks in the mesothorax-prothorax-speaker angles (Middle). Number of peaks in the ears-speaker angles (Bottom).

Chapter 5

Discussion

5.1 Introduction

Insect walking requires the coordination of multiple joints in a single leg to produce various stepping patterns, the coordination of all the legs to produce various gaits and the interaction of the motor output with various sensory inputs and commands from the brain or the other ganglia. The work in this thesis was motivated by the possible interactions between sensory input and motor output in insects. I chose to study cricket phonotactic behaviour as such an example. Previous studies had focused more on the auditory input processing or provided partial information about the body and leg movements. I posed questions derived from the current literature (chapter 2) and I created new tools to obtain data about this behaviour (chapter 3). Furthermore, I provided new information about single leg motion, leg coordination, body angles relative to a sound source and an estimation of the ear's input (chapter 4).

In this chapter, I complete my thesis by discussing the outcome. First, I summarize the contributions I made, as presented in the chapters 3 and 4 (section 5.2). I then suggest some of the future work that could be based on my thesis (section 5.3). Finally, I conclude my thesis with the closing remarks (section 5.4).

5.2 Contributions

- In chapter 3 I presented a new method for studying cricket phonotactic behaviour that produces data on the complete kinematic motions of a freely walking cricket responding to calling song. As well as being novel for crickets, the methods presented here extend the state-of-the-art in insect kinematic analysis in several

ways. The level of detail (full 3D information on all leg joints) has previously been obtained only for tethered animals, of a larger size, with body geometries more amenable to viewing all joints. Moreover I obtain additional information on body articulation, pitch and roll. This is produced by a semi-automated tracking system that compares favourably to that described in Bender et al. (2010) both in terms of overall fitting error and in terms of the rate of user correction required (1-2% of frames vs. 3-5% of frames reported in Bender et al. (2010)). Furthermore, since I avoid using inverse kinematics, I need to mark fewer points in the insect. Marking more points on the legs would be very difficult, if not impossible. The total cost of the experimental setup, including the highspeed cameras (but not the computer) totalled less than £2000. This method allowed me to investigate further the role of each leg pair, each leg and each joint in the walking activity.

- In section 4.2 I presented for the first time in detail the movements of most of the leg and body joints during phonotaxis. Earlier studies provided information either only for the forward walking in the absence of auditory stimulus (Laksanacharoen et al., 2000) or limited information about kinematics in cases where the animal is restricted (Baden and Hedwig, 2008; Witney and Hedwig, 2011). Results from my study include the movement of each joint during right and left turns and forward walking. Some joints contributed more to the change in the patterns of step of each leg. For instance the ThC joints of the front legs play an important role during contralateral turning, while the CTr and FTi joints contribute more during ipsilateral turning. The middle leg's TiTa position is used as a centre for rotation for the insect. Furthermore, I showed that the 3 DoF of the ThC joint and motion of body joints are important for the movement of the cricket, which is something that existing models of insect walking generally neglect in their implementation.

- In section 4.3 I presented for the first time the leg coordination results from the crickets while they performed phonotaxis. Although most of the results agree with existing coordination rules derived from stick insect walking (Cruse et al., 1991), there were some cases that cannot be explained and therefore modification or an alternative methodology has to be followed. For example there were cases when both middle legs were lifted off the ground. Furthermore, I found which legs perform a swing after the transition to the stance phase of another

leg. Context-dependent changes in leg coordination mechanisms have been suggested previously for stick insects (Bläsing and Cruse, 2004; Dürr, 2005; Rosano and Webb, 2007). For example coupling strength for certain rules between the two sides might differ during turning for ipsilateral and contralateral to the turn legs. Further analysis of the results using the methodology discussed in Dürr (2005) could provide more information about specific modifications of the rules.

- In section 4.4 I presented the analysis of the body angles relative to the speaker. These show similar but somewhat smaller deviations from straight walking than previous reports (Weber et al., 1981). For the first time I calculated the angles between the speaker and the ears. This increases the effective angle to sound by 10°-15° compared to the other two body angles. The accuracy of the sound source tracking differs compared to recent experiments on a trackball (Schöneich and Hedwig, 2010). I should note here that the speed of the cricket in these experiments was lower than the speed reported for experiments on a trackball. Previous work has shown that there might be a rapid steering response in every sound pulse when it is presented from alternate directions (Hedwig and Poulet, 2004). One possible reason for this is that depending on the speed of the cricket the local connection between the auditory circuit and the front legs might change its effect. For lower speeds the commands from the brain might play more important role in walking (for instance during initiation of turning, the antennae and the head are the first to move). For higher speeds this local connection might affect more the walking behaviour and therefore contribute to this rapid steering change with reduced involvement of the brain neurons.

- In section 4.5 I estimated for the first time the sound input on both sides as the insect performed phonotaxis, based on the precise position of their ears in the sound field. I also implemented a simulation to estimate the ears input as the insect would walk on a trackball. The results show that the cricket could experience auditory inputs that differ by as much as 4 dB during its step cycle to sound ahead and by as much as 7-8 dB when turning to sound on one side. Comparing ear inputs to corrections in heading suggests a difference of 3-5 dB is needed to cause the animal to correct its course. For the above calculations I used the same delay and gain values for the four sound inputs during the entire walking sequence. Initial data from experiments on a trackball suggest that possible changes in the membrane of the spiracles as the cricket walks might affect

the sound input (Kostarakos et al., 2009). Therefore a possible mechanical connection between the spiracles and the front legs might affect the sound input on the two sides. Another possibility is that there is a neural connection from the sensors of the legs that inhibits the auditory circuit connection to the front legs as described in Baden and Hedwig (2008). This could happen for example in some cases when during a step the sound difference initially becomes larger as the insect moves one of the front legs (figure 4.21).

5.3 Future Research

5.3.1 Experiments

There are several possible improvements or extensions that could be made to this system. During the experiments the cameras are moved manually to follow the insect. It could be possible to motorise this movement, using a third camera that does online tracking of the body position (as one blob) of the insect in the arena. Such systems have already been successfully implemented in our lab, for example, to track flies (Stewart et al., 2010). However, this might cause additional noise and affect the insect's behaviour. Currently the manual tracking needs to ensure the insect does not cover all visible grid points. However, with a motorised system or using distance measuring sensors attached to the cameras, their position could be obtained automatically, which would avoid completely the need for grid marking and tracking. This would be also useful with cameras that do not have large recording memory.

Although I have tried to make the visual environment fairly uniform (white sound proofing, white covers on the speakers) nevertheless it is possible that the cricket in this setup could be combining visual tracking or visual stabilisation with its phonotactic response (Payne et al., 2010). Experiments with infrared light resulted in worse image quality and made the tracking much less reliable. Although some previous reports suggests visual stimuli strongly influence tracking behaviour on the Kramer treadmill (Weber et al., 1981), recent results have not detected dramatic differences in arena tracks produced in the light and the dark (Payne, 2010). It would nevertheless be interesting in this setup to measure more precisely whether phonotaxis tracks are altered in a high contrast visual environment, or if introducing a single visual object elicits visual tracking in competition with tracking of the sound.

Other possible experiments could include the tracking of the abdomen and the end

of the tarsus, since the middle section of the tarsus is the one actually touching the ground in the front and middle legs as the insect moves. However, tracking the tarsus would probably need hand digitization because its small size does not allow it to be painted. Furthermore, tracking the antennae positions through 3D space could give more information about the movements of these sensors and the combination of the two sensory modalities. I only presented sound from one direction in these experiments but it would be interesting to observe the change in the movements of the cricket as it changes its direction. Preliminary results showed that some crickets responded immediately to the change of sound direction, while others stopped when the sound direction changed. Finally, experiments with one of the tympani blocked could show the response or not of the cricket to the sound stimulation.

I only worked on behavioural experiments with the current setup, but in the future it might be possible to combine it with electromyography (Delcomyn and Usherwood, 1973; Watson and Ritzmann, 1997; Sponberg and Full, 2008) or neuron recordings (Pearson, 1972; Takeuchi and Shimoyama, 2004; Keller et al., 2007; Dupuy, 2009). This will offer more insights in the internal functionality of the insect, but may require more precise synchronisation of the cameras. The results presented here indicate which joint angles contribute most to changing leg motion during turns (see section 4.2). Therefore, they suggest which muscles or motor neurons might be best for such a paradigm. Some work towards this direction has been carried out while the cricket walked on a trackball (Baden and Hedwig, 2008).

Finally, it would be ideal to combine methods in order to give more information for each individual cricket. For instance a cricket could first be tested in the arena as presented here, then on a slippery surface (Gruhn et al., 2006; Bender et al., 2010) and a stationary setup for estimating the gains and the delays for the ears (Michelsen et al., 1994). Doing experiments on these setups would give more information on each individual cricket. A slippery surface setup could provide more information on single leg movement, since it decouples the leg relative to the ground. Also, amputations and neurophysiology experiments are easier to perform for a fixed animal. Furthermore, when I estimated the ear's input I assumed that the state of the spiracles remains unchanged during a step cycle. However, the spiracles have a membrane in front of them which is held open with wax during stationary experiments (Michelsen et al., 1994). Maybe a camera zoomed in the specific region could show the state of the spiracle before the insect starts moving and during walking (Kostarakos et al., 2009).

5.3.2 Software

Possible improvements of the software could include a cross-platform version, for example by using the Qt libraries (http://qt.nokia.com/). Furthermore, the performance (*i.e.* processing speed) of the tracking procedure would increase if we integrate it with more powerful graphics processor unit (GPU) functionality. The current version of OpenCV includes an experimental GPU functionality. The use of an optimization algorithm that runs in a GPU would also improve significantly the performance of the model fitting procedure which is the most time-consuming.

Another approach to track the movements of a person has been recently developed (Shotton et al., 2011). It takes into account the possible configurations of the joints of a moving person and trains an algorithm to match each configuration to a given depth map. Since now I know the possible values of the joint of an insect it could be possible to follow a similar approach to track the insect. This would further ease the use of electromyography because it would not be necessary anymore to paint the points of interest on the insect.

5.3.3 Modelling

Based on the results from this work it is possible to extend existing models of cricket phonotaxis, which could be run on a simulated hexapod robot. In order to achieve that the model would have to be able to control joint coordination in the single leg, coordination between all six legs and integrate a neural circuit for auditory processing. Implementations of the auditory circuit exist from previous studies (Webb, 2006, 2008).

First, I would start by modelling a single leg controller. Obviously there would be differences between the three leg pairs. Since there is no detailed information about the neural control of walking in crickets, I would have to base the modelling in current stick insect and cockroach models of locomotion. One possible modelling approach of the single leg controller is the use of individual pattern generators for each joint that are affected by neighbouring joint properties such as the joint angle and load (Ekeberg et al., 2004). Since neurophysiological information is very limited about crickets, I would have to hypothesize possible neural connections between different joints. Parameters to the model could be the angular speed, range of motion and load information. The leg structure should represent as accurately as possible the cricket morphology and therefore include the dimensions of the body and leg segments of the real crickets provided

in table 4.10. Previous models have used only 3 DoF in total for each leg. However, in section 4.2 I demonstrated that all 5 DoF are important for the leg movements. Therefore, an extension of the models need to incorporate these changes. One recent example of such extensions is a 4 DoF cockroach middle leg model (Doorly, 2011). The simulation could be tested first in a kinematic simulation and later on a dynamic simulator such as using Open Dynamics Engine (ODE - www.ode.org), that has been used in earlier studies (Rosano and Webb, 2007). This approach could show the possible implications of the model interacting with the real world properties. The model should not only generate stable walking patterns, but approximate the leg kinematics of the crickets. The evaluation should include leg trajectories and joint angle values.

In order to alter the motion to produce inside or outside turning patterns a change in the effects to the joints should be made. For instance the middle leg CTr joint alters its direction of movements during stance and swing. In phonotaxis, these changes are the output of the auditory processing circuit. It has been suggested from previous trackball results that crickets make a rapid change in heading to every sound pulse (Hedwig and Poulet, 2004). However, as there is no coordination of step cycle with sound pattern, this would imply that the animal must make a very specific adjustment according to the current position of the leg. The front leg effects shown in figure 4.11 are interesting in this regard. If one assumed a sound pulse louder on one side inhibits the ipsilateral ThC joints and contralateral CTr and FTi joints, this could produce the observed change in step motion.

Variations of Cruse's rules (Cruse et al., 1991) have been used in many studies (Espenschied et al., 1993, 1996; Rosano and Webb, 2007; Lewinger and Quinn, 2008). It might be possible to adjust some of the rules to generate gaits similar to the crickets. However, as presented in section 4.2 stance-swing transitions might involve more than FTi extension-flexion transitions. Recent studies regarding leg coordination in stick insects have shown that the movement of one leg can affect the activity of the ThC joints in other two ipsilateral legs (Borgmann et al., 2007, 2009, 2012). Initial simulations have been recently published (Daun-Gruhn and Büschges, 2011; Daun-Gruhn et al., 2012). This further extends the single leg controller I mentioned above to coordinating the three ipsilateral legs. However, more studies will be needed to follow this approach for all six-legs coordination.

5.3.4 Robot Implementation

A robotic model could be used to further understand this biological system (Webb, 2000, 2001, 2006). This will be a neuromechanical model of the cricket, which will be based on a hardware model (physical structure) and a software model (control algorithm). For this purpose, I would have to overcome several technical challenges.

The robot should be designed to represent as accurately as possible cricket morphology, but would need to be on a different scale due to the size of the required motors. The motors should have position and current (load) feedback, such as Dynamixel MX-28 and MX-64 servos (www.robotis.com). Initially, a single leg could be tested. Making a 3 DoFe ThC joint that could handle the weight of the robot would be one of the challenges of the project.

Then the two front legs with a circuit equipped with microphones that simulates the cricket auditory system could be integrated. The noise from the motors would probably affect the input of the microphone sensors. Also the distance between the two FTi joints of the two front legs would be different than the real cricket. Therefore placing microphones on each leg would not create the same system as in crickets. One possible solution would be to place the circuit board responsible for phonotaxis in the front part of the robot similar to (Horchler et al., 2004). However, this configuration would not allow the ears to move as each of the two front legs moves. Alternatively, I could use lower sound frequency for the calling song.

5.4 Conclusion

Clearly there remain a number of technical and algorithmic challenges to be solved before a complete hexapod robot model of cricket phonotaxis could be built. Nevertheless, this thesis provides essential information towards closing the loop between the sensory inputs and motor outputs in this behaviour. By highlighting the key leg motion changes involved in phonotactic turns it points the way for future experimental and simulation work.

Bibliography

Aggarwal, J. K. and Cai, Q. (2002). Human motion analysis: A review. In *Nonrigid and Articulated Motion Workshop, 1997. Proceedings., IEEE*, pages 90–102.

Akay, T., Haehn, S., Schmitz, J., and Büschges, A. (2004). Signals from load sensors underlie interjoint coordination during stepping movements of the stick insect leg. *Journal of Neurophysiology*, 92(1):42–51.

Allen, T. J., Quinn, R. D., Bachmann, R. J., and Ritzmann, R. E. (2003). Abstracted biological principles applied with reduced actuation improve mobility of legged vehicles. In *2003 IEEE/RSJ International Conference on Intelligent Robots and Systems, 2003. (IROS 2003). Proceedings*, volume 2, pages 1370–1375.

Altman, J. and Kien, J. (1987). Functional organization of the subesophageal ganglion in arthropods. In Gupta, A., editor, *Arthropod brain: its evolution, development, structure and function*, pages 265–301. Wiley, New York.

Atkins, G., Chiba, A., Atkins, S., and Stout, J. F. (1988). Low-pass filtering of sound signals by a high-frequency brain neuron and its input in the cricket *Acheta domestica* l. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 164(2):269–276.

Autrum, H. (1958). Electrophysiological analysis of the visual systems in insects. *Experimental Cell Research*, 14(5):426–439.

Baden, T. and Hedwig, B. (2007). Neurite-specific Ca^{2+} dynamics underlying sound processing in an auditory interneurone. *Developmental Neurobiology*, 67(1):68–80.

Baden, T. and Hedwig, B. (2008). Front leg movements and tibial motoneurons underlying auditory steering in the cricket *(Gryllus bimaculatus* de Geer). *Journal of Experimental Biology*, 211(13):2123–2133.

Bailey, W. J. and Thomson, P. (1977). Acoustic orientation in the cricket *Teleogryllus oceanicus* (Le Guillou). *Journal of Experimental Biology*, 67(1):61–75.

Ball, E. E., Oldfield, B. P., and Rudolph, K. M. (1989). Auditory organ structure, development, and function. In Huber, F., Moore, T., and Lohrer, W., editors, *Cricket Behavior and Neurobiology*, pages 391–422. Cornel University Press, Ithaca, NY, US.

Barai, R. K. and Nonami, K. (2007). Optimal two-degree-of-freedom fuzzy control for locomotion control of a hydraulically actuated hexapod robot. *Information Sciences*, 177(8):1892–1915.

Bässler, U. (1988). Functional principles of pattern generation for walking movements of stick insect forelegs: The role of the femoral chordotonal organ afferences. *Journal of Experimental Biology*, 136(1):125–147.

Bässler, U. (1993). The femur-tibia control system of stick insects – a model system for the study of the neural basis of joint control. *Brain Research Reviews*, 18(2):207–226.

Bässler, U. and Büschges, A. (1998). Pattern generation for stick insect walking movements–multisensory control of a locomotor program. *Brain Research. Brain Research Reviews*, 27(1):65–88.

Beer, R. D., Chiel, H. J., Quinn, R. D., Espenschied, K. S., and Larsson, P. (1992). A distributed neural network architecture for hexapod robot locomotion. *Neural Computation*, 4(3):356–365.

Beer, R. D., Chiel, H. J., and Sterling, L. S. (1989). Advances in neural information processing systems 1. chapter Heterogeneous neural networks for adaptive behavior in dynamic environments, pages 577–585.

Bell, W. J. and Kramer, E. (1979). Search and anemotactic orientation of cockroaches. *Journal of Insect Physiology*, 25(8):631–640.

Bender, J. A., Simpson, E. M., and Ritzmann, R. E. (2010). Computer-assisted 3D kinematic analysis of all leg joints in walking insects. *PLoS ONE*, 5(10):e13617.

Bender, J. A., Simpson, E. M., Tietz, B. R., Daltorio, K. A., Quinn, R. D., and Ritzmann, R. E. (2011). Kinematic and behavioral evidence for a distinction between

trotting and ambling gaits in the cockroach *Blaberus discoidalis*. *Journal of Experimental Biology*, 214(12):2057–2064.

Bennet-Clark, H. (1989). Songs and the physics of sound production. In Huber, F., Moore, T., and Lohrer, W., editors, *Cricket Behavior and Neurobiology*, pages 227–261. Cornel University Press, Ithaca, NY, US.

Bennet-Clark, H. C. (1975). The energetics of the jump of the locust schistocerca gregaria. *Journal of Experimental Biology*, 63(1):53–83.

Berns, K., Cordes, S., and Ilg, W. (1994). Adaptive, neural control architecture for the walking machine LAURON. In *Proceedings of the IEEE/RSJ/GI International Conference on Intelligent Robots and Systems '94. 'Advanced Robotic Systems and the Real World', IROS '94*, volume 2, pages 1172–1177. IEEE.

Birch, M., Quinn, R., Hahm, G., Phillips, S., Drennan, B., Fife, A., Verma, H., and Beer, R. (2000). Design of a cricket microrobot. In *Robotics and Automation, 2000. Proceedings. ICRA '00. IEEE International Conference on*, volume 2, pages 1109–1114.

Bläsing, B. and Cruse, H. (2004). Mechanisms of stick insect locomotion in a gap-crossing paradigm. *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology*, 190(3):173–183.

Boggess, M. J., Schroer, R. T., Quinn, R. D., and Ritzmann, R. E. (2004). Mechanized cockroach footpaths enable cockroach-like mobility. In *2004 IEEE International Conference on Robotics and Automation, 2004. Proceedings. ICRA '04*, volume 3, pages 2871–2876.

Böhm, H. and Schildberger, K. (1992). Brain neurones involved in the control of walking in the cricket *Gryllus bimaculatus*. *Journal of Experimental Biology*, 166(1):113–130.

Borgmann, A., Hooper, S. L., and Büschges, A. (2009). Sensory feedback induced by front-leg stepping entrains the activity of central pattern generators in caudal segments of the stick insect walking system. *The Journal of Neuroscience*, 29(9):2972–2983.

Borgmann, A., Scharstein, H., and Büschges, A. (2007). Intersegmental coordination: Influence of a single walking leg on the neighboring segments in the stick insect walking system. *Journal of Neurophysiology*, 98(3):1685–1696.

Borgmann, A., Toth, T. I., Gruhn, M., Daun-Gruhn, S., and Büschges, A. (2012). Dominance of local sensory signals over inter-segmental effects in a motor system: experiments. *Biological cybernetics*, pages 1–13.

Boyan, G. S. (1980). Auditory neurones in the brain of the cricket *Gryllus bimaculatus* (de Geer). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 140(1):81–93.

Boyan, G. S. (1998). Development of the insect auditory system. In Hoy, R. R., Popper, A. N., Fay, R. R., Fay, R. R., and Popper, A. N., editors, *Comparative Hearing: Insects*, volume 10 of *Springer Handbook of Auditory Research*, pages 97–138. Springer New York.

Boyan, G. S. and Williams, J. L. D. (1981). Descending interneurones in the brain of the cricket. anatomy and responses to auditory stimuli. *Naturwissenschaften*, 68(9):486–487.

Boyd, P. and Lewis, B. (1983). Peripheral auditory directionality in the cricket (*Gryllus campestris* L. *Teleogryllus oceanicus* Le Guillou). *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology*, 153(4):523–532.

Bradski, G. and Kaehler, A. (2008). *Learning OpenCV: Computer Vision with the OpenCV Library*. O'Reilly Media Inc, Sebastopol, CA, USA.

Brunn, D. E. and Dean, J. (1994). Intersegmental and local interneurons in the metathorax of the stick insect *Carausius morosus* that monitor middle leg position. *Journal of Neurophysiology*, 72(3):1208–1219.

Büchges, A. (1994). The physiology of sensory cells in the ventral scoloparium of the stick insect femoral chordotonal organ. *Journal of Experimental Biology*, 189(1):285–292.

Burns, M. D. (1973). The control of walking in orthoptera: I. leg movements in normal walking. *Journal of Experimental Biology*, 58(1):45–58.

Burrows, M. (1980). The control of sets of motoneurones by local interneurones in the locust. *Journal of Physiology*, 298(1):213–233.

Burrows, M. (1987). Parallel processing of proprioceptive signals by spiking local interneurons and motor neurons in the locust. *Journal of Neuroscience*, 7(4):1064–1080.

Burrows, M. (1996a). Components of the nervous system: motoneurons. In *The neurobiology of an insect brain*, pages 48–68. Oxford University Press, Oxford, UK.

Burrows, M. (1996b). *The neurobiology of an insect brain*. Oxford University Press, Oxford, UK.

Büschges, A. (1995). Role of local nonspiking interneurons in the generation of rhythmic motor activity in the stick insect. *Journal of Neurobiology*, 27(4):488–512.

Büschges, A., Kittmann, R., and Schmitz, J. (1994). Identified nonspiking interneurons in leg reflexes and during walking in the stick insect. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 174(6):685–700.

Büschges, A., Schmitz, J., and Bässler, U. (1995). Rhythmic patterns in the thoracic nerve cord of the stick insect induced by pilocarpine. *Journal of Experimental Biology*, 198(2):435–456.

Büsghes, A. (1990). Nonspiking pathways in a joint-control loop of the stick insect *Carausius Morosus*. *Journal of Experimental Biology*, 151(1):133–160.

Camhi, J. and Johnson, E. (1999). High-frequency steering maneuvers mediated by tactile cues: antennal wall-following in the cockroach. *Journal of Experimental Biology*, 202(5):631–643.

Camhi, J. M. and Levy, A. (1988). Organization of a complex movement: fixed and variable components of the cockroach escape behavior. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 163(3):317–328.

Carew, T. (2000). *Behavioral neurobiology: the cellular organization of natural behavior*. Sinauer Associates Publishers, Sunderland, MA, USA.

Casaday, G. B. and Hoy, R. R. (1977). Auditory interneurons in the cricket *Teleogryllus oceanicus*: Physiological and anatomical properties. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 121(1):1–13.

Cham, J. G., Bailey, S. A., Clark, J. E., Full, R. J., and Cutkosky, M. R. (2002). Fast and robust: Hexapedal robots via shape deposition manufacturing. *The International Journal of Robotics Research*, 21(10-11):869–882.

Choi, J.-u., Rutter, B. L., Kingsley, D. A., Ritzmann, R. E., and Quinn, R. D. (2005). A robot with cockroach inspired actuation and control. In *Proceedings, 2005 IEEE/ASME International Conference on Advanced Intelligent Mechatronics*, pages 1569–1574. IEEE.

Cohen, M. J. and Jacklet, J. W. (1967). The functional organization of motor neurons in an insect ganglion. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 252(781):561 –569.

Comer, C. M. and Dowd, J. P. (1987). Escape turning behavior of the cockroach. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 160:571–583.

Cowan, N., Ma, E., Cutkosky, M., and Full, R. (2005). A biologically inspired passive antenna for steering control of a running robot. *Robotics Research*, pages 541–550.

Cruse, H. (1976). The function of the legs in the free walking stick insect, *Carausius morosus*. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 112(2):235–262.

Cruse, H. (1985a). Which parameters control the leg movement of a walking insect?: I. velocity control during the stance phase. *Journal of Experimental Biology*, 116(1):343–355.

Cruse, H. (1985b). Which parameters control the leg movement of a walking insect?: II. the start of the swing phase. *Journal of Experimental Biology*, 116(1):357–362.

Cruse, H. (2002). The functional sense of central oscillations in walking. *Biological Cybernetics*, 86:271–280.

Cruse, H. and Bartling, C. (1995). Movement of joint angles in the legs of a walking insect, carausius morosus. *Journal of Insect Physiology*, 41(9):761–771.

Cruse, H., Bartling, C., Cymbalyuk, G., Dean, J., and Dreifert, M. (1995). A modular artificial neural net for controlling a six-legged walking system. *Biological Cybernetics*, 72:421–430.

Cruse, H., Dean, J., Muller, U., and Schmitz, J. (1991). The stick insect as a walking robot. In *Fifth International Conference on Advanced Robotics, 1991. 'Robots in Unstructured Environments', 91 ICAR*, volume 2, pages 936–940. IEEE.

Cruse, H., Dean, J., and Suilmann, M. (1984). The contributions of diverse sense organs to the control of leg movement by a walking insect. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 154(5):695–705.

Cruse, H., Kindermann, T., Schumm, M., Dean, J., and Schmitz, J. (1998). Walknet–a biologically inspired network to control six-legged walking. *Neural Networks*, 11(7-8):1435–1447.

Daun-Gruhn, S. and Büschges, A. (2011). From neuron to behavior: dynamic equation-based prediction of biological processes in motor control. *Biological Cybernetics*, 105(1):71–88.

Daun-Gruhn, S., Toth, T. I., and Borgmann, A. (2012). Dominance of local sensory signals over inter-segmental effects in a motor system: modeling studies. *Biological cybernetics*, pages 1–14.

Dean, J. (1989). Leg coordination in the stick insect *Carausius Morosus*: Effects of cutting thoracic connectives. *Journal of Experimental Biology*, 145(1):103–131.

Delcomyn, F. (1971). The locomotion of the cockroach periplaneta americana. *Journal of Experimental Biology*, 54(2):443–452.

Delcomyn, F. (1980). Neural basis of rhythmic behavior in animals. *Science*, 210(4469):492–498.

Delcomyn, F. (2004). Insect walking and robotics. *Annual Review of Entomology*, 49(1):51–70.

Delcomyn, F. and Nelson, M. E. (2000). Architectures for a biomimetic hexapod robot. *Robotics and Autonomous Systems*, 30(1-2):5–15.

Delcomyn, F. and Usherwood, P. (1973). Motor activity during walking in the cockroach *Periplaneta americana*. *Journal of Experimental Biology*, 59(3):629–642.

Doherty, J. A. (1985). Temperature coupling and "trade-off" phenomena in the acoustic communication system of the cricket, *Gryllus bimaculatus* de Geer (Gryllidae). *Journal of Experimental Biology*, 114(1):17–35.

Doherty, J. A. (1991). Song recognition and localization in the phonotaxis behavior of the field cricket, *Gryllus bimaculatus* (Orthoptera: gryllidae). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 168.

Doorly, N. C. (2011). A neuromechanical model for cockroach locomotion. Master's thesis, Case Western Reserve University.

Dupuy, F. (2009). *La perception des mouvements d'air par le système cercal chez le grillon des bois Nemobius sylvestris*. PhD thesis, Université François Rabelais - Tours.

Dürr, V. (2001). Stereotypic leg searching movements in the stick insect: Kinematic analysis, behavioural context and simulation. *Journal of Experimental Biology*, 204(9):1589–1604.

Dürr, V. (2005). Context-dependent changes in strength and efficacy of leg coordination mechanisms. *Journal of Experimental Biology*, 208(12):2253–2267.

Dürr, V. and Ebeling, W. (2005). The behavioural transition from straight to curve walking: kinetics of leg movement parameters and the initiation of turning. *Journal of Experimental Biology*, 208(12):2237–2252.

Eibl, E. (1978). Morphology of the sense organs in the proximal parts of the tibiae of *Gryllus campestris* L. and *Gryllus bimaculatus* de Geer (Insecta, Ensifera). *Zoomorphologie*, 89(3):185–205.

Ekeberg, O., Blümel, M., and Büschges, A. (2004). Dynamic simulation of insect walking. *Arthropod Structure & Development*, 33(3):287–300.

Epstein, S. and Graham, D. (1983). Behaviour and motor output of stick insects walking on a slippery surface: I. forward walking. *Journal of Experimental Biology*, 105(1):215–229.

Espenschied, K. S., Chiel, H. J., Quinn, R. D., and Beer, R. D. (1993). Leg coordination mechanisms in the stick insect applied to hexapod robot locomotion. *Adaptive Behavior*, 1(4):455–468.

Espenschied, K. S., Quinn, R. D., Beer, R. D., and Chiel, H. J. (1996). Biologically based distributed control and local reflexes improve rough terrain locomotion in a hexapod robot. *Robotics and Autonomous Systems*, 18(1-2):59–64.

Fraenkel, G. S. and Gunn, D. L. (1940). *The orientation of animals: Kineses, taxes and compass reactions*. Oxford University Press, Oxford, UK.

Franklin, R., Bell, W. J., and Jander, R. (1981). Rotational locomotion by the cockroach *Blattella germanica*. *Journal of Insect Physiology*, 27(4):249–255.

Franks, N., Wilby, A., Silverman, B., and Tofts, C. (1992). Self-organizing nest construction in ants: sophisticated building by blind bulldozing. *Animal Behaviour*, 44, Part 2(0):357–375.

Frantsevich, L. I. and Mokrushov, P. A. (1980). Turning and righting in *Geotrupes* (Coleoptera, Scarabaeidae). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 136(4):279–289.

Frik, M., Guddat, M., Losch, D., and Karatas, M. (1998). Terrain adaptive control of the walking machine Tarry II. In *Proc. European Mechanics Colloquium, Euromech*, volume 375, pages 108–115.

Gassmann, B., Scholl, K. U., and Berns, K. (2001). Locomotion of LAURON III in rough terrain. In *2001 IEEE/ASME International Conference on Advanced Intelligent Mechatronics, 2001. Proceedings*, volume 2, pages 959–964. IEEE.

Gebhardt, M. and Honegger, H. (2001). Physiological characterisation of antennal mechanosensory descending interneurons in an insect (*Gryllus bimaculatus*, *Gryllus campestris*) brain. *Journal of Experimental Biology*, 204(13):2265–2275.

Gnatzy, W. and Hustert, R. (1989). Mechanoreceptors in Behavior. In Huber, F., Moore, T., and Lohrer, W., editors, *Cricket Behavior and Neurobiology*, pages 198–226. Cornel University Press, Ithaca, NY, US.

Graham, D. (1972). A behavioural analysis of the temporal organisation of walking movements in the 1st instar and adult stick insect (*Carausius morosus*). *Journal of*

Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology, 81:23–52.

Gruhn, M., Hoffmann, O., Dübbert, M., Scharstein, H., and Büschges, A. (2006). Tethered stick insect walking: A modified slippery surface setup with optomotor stimulation and electrical monitoring of tarsal contact. *Journal of Neuroscience Methods*, 158(2):195–206.

Gruhn, M., Zehl, L., and Büschges, A. (2009). Straight walking and turning on a slippery surface. *Journal of Experimental Biology*, 212(2):194–209.

Hager, W. W. and Zhang, H. (2006). A new active set algorithm for box constrained optimization. *SIAM Journal on Optimization*, 17(2):526–557.

Harris, J. and Ghiradella, H. (1980). The forces exerted on the substrate by walking and stationary crickets. *Journal of Experimental Biology*, 85(1):263–279.

Hedrick, T. L. (2008). Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspiration & Biomimetics*, 3(3):034001.

Hedwig, B. (1994). A cephalothoracic command system controls stridulation in the acridid grasshopper omocestus viridulus l. *Journal of Neurophysiology*, 72(4):2015–2025.

Hedwig, B. (2000). Control of cricket stridulation by a command neuron: Efficacy depends on the behavioral state. *Journal of Neurophysiology*, 83(2):712–722.

Hedwig, B. (2006). Pulses, patterns and paths: neurobiology of acoustic behaviour in crickets. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 192(7):677–689.

Hedwig, B. and Poulet, J. F. A. (2004). Complex auditory behaviour emerges from simple reactive steering. *Nature*, 430(7001):781–5.

Heinrich, R. (2002). Impact of descending brain neurons on the control of stridulation, walking, and flight in orthoptera. *Microscopy Research and Technique*, 56(4):292–301.

Heitler, W. J. and Burrows, M. (1977). The locust jump. i. the motor programme. *Journal of Experimental Biology*, 66(1):203–219.

Hennig, R. M. (1988). Ascending auditory interneurons in the cricket *Teleogryllus commodus* (Walker): comparative physiology and direct connections with afferents. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 163(1):135–143.

Hennig, R. M. (2003). Acoustic feature extraction by cross-correlation in crickets? *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 189(8):589–598.

Hess, D. and Büschges, A. (1997). Sensorimotor pathways involved in interjoint reflex action of an insect leg. *Journal of Neurobiology*, 33(7):891–913.

Hess, D. and Büschges, A. (1999). Role of proprioceptive signals from an insect femur-tibia joint in patterning motoneuronal activity of an adjacent leg joint. *Journal of Neurophysiology*, 81(4):1856–1865.

Hestenes, M. and Stiefel, E. (1952). Methods of conjugate gradients for solving linear systems. *ournal of Research of the National Bureau of Standards*, 49:409–436.

Hofmann, T., Koch, U., and Bässler, U. (1985). Physiology of the femoral chordotonal organ in the stick insect, *Cuniculina impigra*. *Journal of Experimental Biology*, 114(1):207–223.

Horchler, A. D., Reeve, R. E., Webb, B., and Quinn, R. D. (2004). Robot phonotaxis in the wild: a biologically inspired approach to outdoor sound localization. *Advanced Robotics*, 18(8):801–816.

Horn, E. and Bischof, H. (1983). Gravity reception in crickets: The influence of cereal and antennal afferences on the head position. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 150(1):93–98.

Horn, E. and Föller, W. (1985). Tonic and modulatory subsystems of the complex gravity receptor system in crickets, *Gryllus bimaculatus*. *Journal of Insect Physiology*, 31(12):937–946.

Horseman, G. and Huber, F. (1994). Sound localisation in crickets. i. contralateral inhibition of an ascending auditory interneuron (AN1) in the cricket *Gryllus bimaculatus*. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 175(4):389–398.

Hoy, R. R. (1978). Acoustic communication in crickets: a model system for the study of feature detection. *Federation Proceedings*, 37(10):2316–2323.

Hoy, R. R. and Paul, R. C. (1973). Genetic control of song specificity in crickets. *Science*, 180(4081):82–83.

Huber, F. (1960). Untersuchungen über die funktion des zentralnervensystems und insbesondere des gehirnes bei der fortbewegung und der lauterzeugung der grillen. *Zeitschrift für Vergleichende Physiologie*, 44(1):60–132.

Huber, F. and Thorson, J. (1985). Cricket auditory communication. *Scientific American*, 253(6):60–68.

Hughes, G. M. (1952). The Co-Ordination of insect movements i the walking movements of insects. *Journal of Experimental Biology*, 29(2):267–285.

Ilg, W. and Berns, K. (1995). A learning architecture based on reinforcement learning for adaptive control of the walking machine LAURON. *Robotics and Autonomous Systems*, 15(4):321–334.

Jindrich, D. and Full, R. (1999). Many-legged maneuverability: dynamics of turning in hexapods. *Journal of Experimental Biology*, 202(12):1603–1623.

Kalman, R. E. (1960). A new approach to linear filtering and prediction problems. *Journal of Basic Engineering*, 82(1):35–45.

Keller, B. R., Duke, E. R., Amer, A. S., and Zill, S. N. (2007). Tuning posture to body load: decreases in load produce discrete sensory signals in the legs of freely standing cockroaches. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 193(8):881–891.

Kennedy, J. S. and Marsh, D. (1974). Pheromone-Regulated anemotaxis in flying moths. *Science*, 184(4140):999–1001.

Kien, J. (1983). The initiation and maintenance of walking in the locust: An alternative to the command concept. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, 219(1215):137–174.

Kien, J. (1990a). Neuronal activity during spontaneous walking–I. starting and stopping. *Comparative Biochemistry and Physiology Part A: Physiology*, 95(4):607–621.

Kien, J. (1990b). Neuronal activity during spontaneous walking–II. correlation with stepping. *Comparative Biochemistry and Physiology Part A: Physiology*, 95(4):623–638.

Kostarakos, K., Hennig, M. R., and Römer, H. (2009). Two matched filters and the evolution of mating signals in four species of cricket. *Frontiers in Zoology*, 6(1):1–12.

Kostarakos, K. and Römer, H. (2010). Sound transmission and directional hearing in field crickets: neurophysiological studies outdoors. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 196:669–681.

Kram, R., Wong, B., and Full, R. J. (1997). Three-dimensional kinematics and limb kinetic energy of running cockroaches. *Journal of Experimental Biology*, 200(13):1919–1929.

Kupfermann, I. and Weiss, K. R. (1978). The command neuron concept. *Behavioral and Brain Sciences*, 1(1):3–10.

Kutsch, W. and Huber, F. (1989). Neural basis of song production. In Huber, F., Moore, T., and Lohrer, W., editors, *Cricket Behavior and Neurobiology*, pages 262–309. Cornel University Press, Ithaca, NY, US.

Laksanacharoen, S., Pollack, A. J., Nelson, G. M., Quinn, R. D., and Ritzmann, R. E. (2000). Biomechanics and simulation of cricket for microrobot design. In *Robotics and Automation, 2000. Proceedings. ICRA'00. IEEE International Conference on*, volume 2, pages 1088–1094.

Laksanacharoen, S., Quinn, R., and Ritzmann, R. (2003). Modeling of insect's legs by inverse kinematics analysis. In *Proceedings of the 2nd International Symposium on Adaptive Motion of Animals and Machines*, pages 4–8.

Larsen, G., Frazier, S., Fish, S., and Zill, S. (1995). Effects of load inversion in cockroach walking. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 176(2):229–238.

Larsen, O., Kleindienst, H., and Michelsen, A. (1989). Biophysical aspects of sound reception. In Huber, F., Moore, T., and Lohrer, W., editors, *Cricket Behavior and Neurobiology*, pages 364–390. Cornel University Press, Ithaca, NY, US.

Larsen, O. N. (1987). The cricket's anterior tympanum revisited. *Naturwissenschaften*, 74(2):92–94.

Laurent, G. and Burrows, M. (1989). Distribution of intersegmental inputs to nonspiking local interneurons and motor neurons in the locust. *Journal of Neuroscience*, 9(9):3019–3029.

Laurent, G. and Richard, D. (1986a). The organization and role during locomotion of the proximal musculature of the cricket foreleg: I. Anatomy and innervation. *Journal of Experimental Biology*, 123(1):255–283.

Laurent, G. and Richard, D. (1986b). The organization and role during locomotion of the proximal musculature of the cricket foreleg: II. Electromyographic activity during stepping patterns. *Journal of Experimental Biology*, 123(1):285–306.

Lewinger, W., Rutter, B., Blumel, M., Büschges, A., and Quinn, R. (2006). Sensory coupled action switching modules (scasm) generate robust, adaptive stepping in legged robots. In *International Conference on Climbing and Walking Robots*, volume 2006, pages 661–671, Brussels, Belgium.

Lewinger, W. A. and Quinn, R. D. (2008). BILL-LEGS: low computation emergent gait system for small mobile robots. In *IEEE International Conference on Robotics and Automation, 2008. ICRA 2008*, pages 251–256. IEEE.

Lewinger, W. A. and Quinn, R. D. (2009). A small, autonomous, agile robot with an on-board, neurobiologically-based control system. In *IEEE/RSJ International Conference on Intelligent Robots and Systems, 2009. IROS 2009*, pages 412–413. IEEE.

Loher, W., Weber, T., and Huber, F. (1993). The effect of mating on phonotactic behaviour in *Gryllus bimaculatus* (de Geer). *Physiological Entomology*, 18(1):57–66.

Ludwar, B., Göritz, M. L., and Schmidt, J. (2005). Intersegmental coordination of walking movements in stick insects. *Journal of Neurophysiology*, 93(3):1255–1265.

Lund, H. H., Webb, B., and Hallam, J. (1997). A robot attracted to the cricket species *Gryllus bimaculatus*. In *Proceedings of the Fourth European Conference on Artificial Life*, pages 131–140.

Mason, A. C., Lee, N., and Oshinsky, M. L. (2005). The start of phonotactic walking in the fly *Ormia ochracea*: a kinematic study. *Journal of Experimental Biology*, 208(24):4699–4708.

Matsumoto, Y. and Mizunami, M. (2002). Temporal determinants of long-term retention of olfactory memory in the cricket *Gryllus bimaculatus*. *Journal of Experimental Biology*, 205(10):1429–1437.

Maye, A., Hsieh, C.-h., Sugihara, G., and Brembs, B. (2007). Order in spontaneous behavior. *PLoS ONE*, 2(5):e443.

Mhatre, N. and Balakrishnan, R. (2007). Phonotactic walking paths of field crickets in closed-loop conditions and their simulation using a stochastic model. *Journal of Experimental Biology*, 210(20):3661–3676.

Michel, K. (1974). Das tympanalorgan von *Gryllus bimaculatus* degeer (saltatoria, gryllidae). *Zeitschrift für Morphologie der Tiere*, 77:285–315.

Michelsen, A., Popov, A., and Lewis, B. (1994). Physics of directional hearing in the cricket *Gryllus bimaculatus*. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 175(2):153–164.

Mu, L. and Ritzmann, R. E. (2005). Kinematics and motor activity during tethered walking and turning in the cockroach, *Blaberus discoidalis*. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 191(11):1037–1054.

Murphey, R. K. and Zaretsky, M. D. (1972). Orientation to calling song by female crickets, *Scapsipedus marginatus* (Gryllidae). *Journal of Experimental Biology*, 56(2):335–352.

Nabatiyan, A., Poulet, J., de Polavieja, G. G., and Hedwig, B. (2003). Temporal pattern recognition based on instantaneous spike rate coding in a simple auditory system. *Journal of Neurophysiology*, 90(4):2484–2493.

Nishino, H. (2000). Topographic mapping of the axons of the femoral chordotonal organ neurons in the cricket *Gryllus bimaculatus*. *Cell and Tissue Research*, 299(1):145–157.

Nishino, H. (2003). Local innervation patterns of the metathoracic flexor and extensor tibiae motor neurons in the cricket *Gryllus bimaculatus*. *Zoological Science*, 20(6):697–707.

Nishino, H. and Sakai, M. (1997). Three neural groups in the femoral chordotonal organ of the cricket *Gryllus bimaculatus*: central projections and soma arrangement and displacement during joint flexion. *Journal of Experimental Biology*, 200(20):2583–2595.

Nowel, M., Shelton, P., and Stephen, R. (1995). Functional organisation of the metathoracic femoral chordotonal organ in the cricket *Acheta domesticus*. *Journal of Experimental Biology*, 198(9):1977–1988.

Nye, S. W. and Ritzmann, R. E. (1992). Motion analysis of leg joints associated with escape turns of the cockroach, *Periplaneta americana*. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 171(2):183–194.

Olberg, R., Worthington, A., and Venator, K. (2000). Prey pursuit and interception in dragonflies. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 186(2):155–162.

Payne, M. (2010). *Co-ordinating Behaviours in an Insect Biorobot*. PhD thesis, University of Edinburgh.

Payne, M., Hedwig, B., and Webb, B. (2010). Multimodal predictive control in crickets. In Doncieux, S., Girard, B., Guillot, A., Hallam, J., Meyer, J.-A., and Mouret, J.-B., editors, *From Animals to Animats 11*, volume 6226 of *Lecture Notes in Computer Science*, pages 167–177. Springer Berlin / Heidelberg.

Pearson, K. G. (1972). Central programming and reflex control of walking in the cockroach. *Journal of Experimental Biology*, 56(1):173–193.

Pearson, K. G. and Fourtner, C. R. (1975). Nonspiking interneurons in walking system of the cockroach. *Journal of Neurophysiology*, 38(1):33–52.

Pearson, K. G. and Iles, J. F. (1973). Nervous mechanisms underlying intersegmental Co-Ordination of leg movements during walking in the cockroach. *Journal of Experimental Biology*, 58(3):725–744.

Petrou, G. and Webb, B. (2012). Detailed tracking of body and leg movements of a freely walking female cricket during phonotaxis. *Journal of Neuroscience Methods*, 203(1):56–68.

Pfeiffer, F., Eltze, J., and Weidemann, H. (1995). Six-legged technical walking considering biological principles. *Robotics and Autonomous Systems*, 14(2-3):223–232.

Pollack, G. S. and Hoy, R. R. (1979). Temporal pattern as a cue for species-specific calling song recognition in crickets. *Science*, 204(4391):429–432.

Popov, A. V. and Markovich, A. M. (1982). Auditory interneurones in the prothoracic ganglion of the cricket, *Gryllus bimaculatus*. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 146(3):351–359.

Popov, A. V., Markovich, A. M., and Andjan, A. S. (1978). Auditory interneurons in the prothoracic ganglion of the cricket, *Gryllus bimaculatus* DeGeer. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 126(2):183–192.

Popov, A. V. and Shuvalov, V. F. (1977). Phonotactic behavior of crickets. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 119(1):111–126.

Poulet, J. F. A. and Hedwig, B. (2005). Auditory orientation in crickets: Pattern recognition controls reactive steering. *Proceedings of the National Academy of Sciences of the United States of America*, 102(43):15665–15669.

Quinn, R. and Ritzmann, R. (1998). Construction of a hexapod robot with cockroach kinematics benefits both robotics and biology. *Connection Science*, 10(3):239–254.

Reeve, R., Schaik, A. v., Jin, C., Hamilton, T., Torben-Nielsen, B., and Webb, B. (2007). Directional hearing in a silicon cricket. *BioSystems*, 87(2-3):307–313.

Reeve, R. E. and Webb, B. H. (2003). New neural circuits for robot phonotaxis. *Philosophical Transactions of the Royal Society of London A*, 361(1811):2245–2266.

Regen, J. (1913). Üeber die anlockung des weibchens von *Gryllus campestris* durch telephonische übertragung der stridulation des männchens. *Pflügers Archiv European Journal of Physiology*, 155(1):193–200.

Rheinlaender, J. and Blätgen, G. (1982). The precision of auditory lateralization in the cricket, *Gryllus bimaculatus*. *Physiological Entomology*, 7(2):209–218.

Ridgel, A., Alexander, B., and Ritzmann, R. (2007). Descending control of turning behavior in the cockroach, *Blaberus discoidalis*. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 193(4):385–402.

Römer, H. (1993). Environmental and biological constraints for the evolution of Long-Range signalling and hearing in acoustic insects. *Royal Society of London Philosophical Transactions Series B*, 340:179–185.

Rosano, H. and Webb, B. (2007). A dynamic model of thoracic differentiation for the control of turning in the stick insect. *Biological Cybernetics*, 97(3):229–246.

Rutter, B., Taylor, B., Bender, J., Blumel, M., Lewinger, W., Ritzmann, R., and Quinn, R. (2011). Descending commands to an insect leg controller network cause smooth behavioral transitions. In *Intelligent Robots and Systems (IROS), 2011 IEEE/RSJ International Conference on*, pages 215–220.

Ryckebusch, S. and Laurent, G. (1993). Rhythmic patterns evoked in locust leg motor neurons by the muscarinic agonist pilocarpine. *Journal of Neurophysiology*, 69(5):1583–1595.

Saranli, U., Buehler, M., and Koditschek, D. E. (2001). RHex: a simple and highly mobile hexapod robot. *The International Journal of Robotics Research*, 20(7):616–631.

Schildberger, K. (1984a). Multimodal interneurons in the cricket brain: properties of identified extrinsic mushroom body cells. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 154(1):71–79.

Schildberger, K. (1984b). Temporal selectivity of identified auditory neurons in the cricket brain. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 155(2):171–185.

Schildberger, K. (1988). Behavioral and neuronal mechanisms of cricket phonotaxis. *Cellular and Molecular Life Sciences (CMLS)*, 44(5):408–415.

Schildberger, K. and Hörner, M. (1988). The function of auditory neurons in cricket phonotaxis. I. influence of hyperpolarization of identified neurons on sound localization. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 163:621–631.

Schildberger, K., Huber, F., and Wohlers, D. W. (1989). Central auditory pathway: neuronal correlates of phonotactic behavior. In Huber, F., Moore, T., and Lohrer, W., editors, *Cricket Behavior and Neurobiology*, pages 423–458. Cornel University Press, Ithaca, NY, US.

Schilling, M., Cruse, H., and Arena, P. (2007). Hexapod walking: an expansion to walknet dealing with leg amputations and force oscillations. *Biological Cybernetics*, 96:323–340.

Schmitz, B., Scharstein, H., and Wendler, G. (1982). Phonotaxis in *Gryllus campestris* l. (orthoptera, gryllidae). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 148:431–444.

Schneider, A., Cruse, H., and Schmitz, J. (2005). A biologically inspired active compliant joint using local positive velocity feedback (LPVF). *IEEE Transactions on Systems, Man, and Cybernetics, Part B: Cybernetics*, 35(6):1120–1130.

Schneider, A., Cruse, H., and Schmitz, J. (2006). Decentralized control of elastic limbs in closed kinematic chains. *The International Journal of Robotics Research*, 25(9):913–930.

Schöneich, S. and Hedwig, B. (2010). Hyperacute directional hearing and phonotactic steering in the cricket (*Gryllus bimaculatus* de geer). *PLoS ONE*, 5(12):e15141.

Selverston, A., Kleindienst, H., and Huber, F. (1985). Synaptic connectivity between cricket auditory interneurons as studied by selective photoinactivation. *Journal of Neuroscience*, 5(5):1283–1292.

Shotton, J., Fitzgibbon, A., Cook, M., Sharp, T., Finocchio, M., Moore, R., Kipman, A., and Blake, A. (2011). Real-time human pose recognition in parts from single depth images. In *CVPR*, volume 2, page 3.

Siegler, M. V. (1981). Postural changes alter synaptic interactions between nonspiking interneurons and motor neurons of the locust. *Journal of Neurophysiology*, 46(2):310–323.

Siegler, M. V. S. and Pousman, C. A. (1990). Distribution of motor neurons into anatomical groups in the grasshopper metathoracic ganglion. *Journal of Comparative Neurology*, 297(2):313–327.

Simmons, L. (1990). Post-copulatory guarding, female choice and the levels of gregarine infections in the field cricket, *Gryllus bimaculatus*. *Behavioral Ecology and Sociobiology*, 26:403–407.

Sponberg, S. and Full, R. (2008). Neuromechanical response of musculo-skeletal structures in cockroaches during rapid running on rough terrain. *Journal of Experimental Biology*, 211(3):433–446.

Srinivasan, M., Zhang, S., Altwein, M., and Tautz, J. (2000). Honeybee navigation: nature and calibration of the "odometer". *Science*, 287(5454):851–853.

Stabel, J., Wendler, G., and Scharstein, H. (1989). Cricket phonotaxis: localization depends on recognition of the calling song pattern. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 165(2):165–177.

Staudacher, E. (1998). Distribution and morphology of descending brain neurons in the cricket *Gryllus bimaculatus*. *Cell and Tissue Research*, 294(1):187–202.

Staudacher, E. and Schildberger, K. (1998). Gating of sensory responses of descending brain neurones during walking in crickets. *Journal of Experimental Biology*, 201(4):559–572.

Staudacher, E. M. (2001). Sensory responses of descending brain neurons in the walking cricket, *Gryllus bimaculatus*. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 187(1):1–17.

Stewart, F. J., Baker, D. A., and Webb, B. (2010). A model of visual-olfactory integration for odour localisation in free-flying fruit flies. *Journal of Experimental Biology*, 213(11):1886–1900.

Stout, J. F., DeHaan, C. H., and McGhee, R. W. (1983). Attractiveness of the male *Acheta domesticus* calling song to females. i. dependence on each of the calling song features. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 153(4):509–521.

Stout, J. F. and McGhee, R. W. (1988). Attractiveness of the male *Acheta domesticus* calling song to females. II. The relative importance of syllable period, intensity and chirp rate. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 164(4):277–287.

Strauss, R. and Heisenberg, M. (1990). Coordination of legs during straight walking and turning in *Drosophila melanogaster*. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 167(3):403–412.

Takeuchi, S. and Shimoyama, I. (2004). A radio-telemetry system with a shape memory alloy microelectrode for neural recording of freely moving insects. *IEEE Transactions on Biomedical Engineering*, 51(1):133–137.

Thorson, J., Weber, T., and Huber, F. (1982). Auditory behavior of the cricket. II. Simplicity if calling song recognition in *Gryllus*, and anomalous phonotaxis at abnormal carrier frequencies. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 146:361–378.

Tryba, A. K. and Ritzmann, R. E. (2000). Multi-Joint coordination during walking and foothold searching in the *Blaberus* cockroach. I. kinematics and electromyograms. *Journal of Neurophysiology*, 83(6):3323–3336.

Von Frisch, K. (1967). *The dance language and orientation of bees*. Harvard University Press, Cambridge, MA, US.

von Twickel, A., Büschges, A., and Pasemann, F. (2011). Deriving neural network controllers from neuro-biological data: implementation of a single-leg stick insect controller. *Biological Cybernetics*, 104(1-2):95–119.

von Twickel, A., Hild, M., Siedel, T., Patel, V., and Pasemann, F. (2012). Neural control of a modular multi-legged walking machine: Simulation and hardware. *Robotics and Autonomous Systems*, 60(2):227–241.

Walker, T. J. and Masaki, S. (1989). Natural history. In Huber, F., Moore, T., and Lohrer, W., editors, *Cricket Behavior and Neurobiology*, pages 1–42. Cornel University Press, Ithaca, NY, US.

Watson, A. H. D., Burrows, M., and Hale, J. P. (1985). The morphology and ultrastructure of common inhibitory motor neurones in the thorax of the locust. *Journal of Comparative Neurology*, 239(3):341–359.

Watson, J. T. and Ritzmann, R. E. (1997). Leg kinematics and muscle activity during treadmill running in the cockroach, *Blaberus discoidalis*: I. slow running. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 182(1):11–22.

Watson, J. T., Ritzmann, R. E., Zill, S. N., and Pollack, A. J. (2002). Control of obstacle climbing in the cockroach, *Blaberus discoidalis*. I. Kinematics. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 188(1):39–53.

Webb, B. (1995). Using robots to model animals: a cricket test. *Robotics and Autonomous Systems*, 16(2-4):117–134.

Webb, B. (2000). What does robotics offer animal behaviour? *Animal Behaviour*, 60(5):545–558.

Webb, B. (2001). Can robots make good models of biological behaviour? *Behavioral and brain sciences*, 24:1033–1050.

Webb, B. (2006). Validating biorobotic models. *Journal of Neural Engineering*, 3(3):R25–R35.

Webb, B. (2008). Spiking neuron controllers for a sound localising robot. In Arena, P., Pfeiffer, F., Rammerstorfer, F. G., Salenon, J., Schrefler, B., and Serafini, P., editors, *Dynamical Systems, Wave-Based Computation and Neuro-Inspired Robots*, volume 500 of *CISM Courses and Lectures*, pages 119–130. Springer Vienna.

Webb, B. and Scutt, T. (2000). A simple latency-dependent spiking-neuron model of cricket phonotaxis. *Biological Cybernetics*, 82(3):247–269.

Weber, T. and Thorson, J. (1989). Phonotactic behavior of walking crickets. In Huber, F., Moore, T., and Lohrer, W., editors, *Cricket Behavior and Neurobiology*, pages 310–339. Cornel University Press, Ithaca, NY, USA.

Weber, T., Thorson, J., and Huber, F. (1981). Auditory behavior of the cricket. I. Dynamics of compensated walking and discrimination paradigms on the kramer treadmill. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 141(2):215–232.

Wehner, R. (2003). Desert ant navigation: how miniature brains solve complex tasks. *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology*, 189:579–588.

Weidemann, H. J., Pfeiffer, F., and Eltze, J. (1993). A design concept for legged robots derived from the walking stick insect. In *Proceedings of the 1993 IEEE/RSJ International Conference on Intelligent Robots and Systems '93, IROS '93*, volume 1, pages 545–552. IEEE.

Weidemann, H. J., Pfeiffer, F., and Eltze, J. (1994). The six-legged TUM walking robot. In *Proceedings of the IEEE/RSJ/GI International Conference on Intelligent Robots and Systems '94. 'Advanced Robotic Systems and the Real World', IROS '94*, volume 2, pages 1026–1033. IEEE.

Wendler, G. (1990). Pattern recognition and localization in cricket phonotaxis. In Gribakin, G., Wiese, K., and Popov, A., editors, *Sensory systems and communication in arthropods*, pages 387–394. Basel: Birkhäuser.

Wiese, K. (1981). Influence of vibration on cricket hearing: Interaction of low frequency vibration and acoustic stimuli in the omega neuron. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 143(1):135–142.

Wiese, K. and Eilts, K. (1985). Evidence for matched frequency dependence of bilateral inhibition in the auditory pathway of *Gryllus bimaculatus*. *Zoologische Jahrbücher*, 89(2):181–201.

Witney, A. G. and Hedwig, B. (2011). Kinematics of phonotactic steering in the walking cricket *Gryllus bimaculatus* (de Geer). *Journal of Experimental Biology*, 214(1):69–79.

Wohlers, D. W. and Huber, F. (1978). Intracellular recording and staining of cricket auditory interneurons *Gryllus campestris* L., *Gryllus bimaculatus* DeGeer). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 127(1):11–28.

Wohlers, D. W. and Huber, F. (1982). Processing of sound signals by six types of neurons in the prothoracic ganglion of the cricket *Gryllus campestris* L. *Journal of*

Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology, 146(2):161–173.

Wolf, H. and Laurent, G. (1994). Rhythmic modulation of the responsiveness of locust sensory local interneurons by walking pattern generating networks. *Journal of Neurophysiology*, 71(1):110–118.

Yoneda, K. and Ota, Y. (2003). Non-Bio-Mimetic walkers. *The International Journal of Robotics Research*, 22(3-4):241–249.

Zakotnik, J., Matheson, T., and Dürr, V. (2004). A posture optimization algorithm for model-based motion capture of movement sequences. *Journal of Neuroscience Methods*, 135(1-2):43–54.

Zhang, Y., Huang, H., Liu, X., and Ren, L. (2011). Kinematics of terrestrial locomotion in mole cricket *Gryllotalpa orientalis*. *Journal of Bionic Engineering*, 8(2):151–157.

Zill, S. N. (1986). A model of pattern generation of cockroach walking reconsidered. *Journal of Neurobiology*, 17(4):317–328.

Zollikofer, C. P. E. (1994). Stepping patterns in ants. I. Influence of speed and curvature. *Journal of Experimental Biology*, 192(1):95–106.

Zolotov, V., Frantsevich, L., and Falk, E. M. (1975). Kinematik der phototaktischen drehung bei der honigbiene *Apis mellifera* L. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 97(4):339–353.

Zorovic, M. and Hedwig, B. (2011). Processing of species-specific auditory patterns in the cricket brain by ascending, local, and descending neurons during standing and walking. *Journal of Neurophysiology*, 105(5):2181–2194.